Challenges and opportunities for aquatic ecosystem management with uncertain global change

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Abstract

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Society is faced with the task of effectively managing to enable ecosystem resilience to anthropogenic stressors and future change. Ecosystems are part of complex social-ecological systems where humans impact ecosystems and anthropogenic change and natural variability feed back to impact people. Management of ecosystems also involves balancing different ecosystem services and values that people place on ecosystems. These complex challenges for the management of social-ecological systems require interdisciplinary approaches that address these challenges from multiple scales.

In this dissertation, I examine patterns and processes in ecosystems and social-ecological systems that may provide opportunities for management to overcome some of the challenges for the future. In chapter one, I assess how multiple stressors impact the life cycle of a commercially important fish species and demonstrate that multiple stressors impact important life-history complexity with implications for population stability. These changes may make populations less

reliable for commercial fisheries. In the second chapter, I evaluate the interaction between two competing ecosystem services and show that common ecological processes including density-dependence and population stochasticity reduce the strength of the interaction between them and render multiple benefits from ecosystems with a relatively simple management strategy. In my third chapter, I examine how population density and stream habitat characteristics interact to influence the habitat usage of sockeye salmon on the spawning grounds, which can alter their ecological benefit to freshwater ecosystems and the effectiveness of habitat restoration. In my final chapter, I explore how human communities can exploit complexity in the natural environment to buffer against uncertainty and catastrophic shifts in social-ecological systems.

This work takes an interdisciplinary approach to addressing these challenges for management. The research spans multiple scales from species to ecosystems and incorporates humans in complex social-ecological systems. Management of ecosystems is challenging due to the immense amount of complexity. However, complexity in nature can provide stability and opportunities for management to take advantage of to improve management outcomes given uncertain global change.

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General Introduction

Humans are intimately tied to the natural world, relying heavily on many services provided by ecosystems. However, human activities impact ecosystems in many ways (Vitousek *et al.* 1997), which can change the delivery of the services we depend upon. Management of ecosystems and their associated services is challenged by increasing rates of exploitation, numerous anthropogenic stressors, and considerable natural variability. The most common approach for confronting these challenges is through reductionist approaches to understanding ecosystems to predict and prescribe management solutions for the future (Levins and Lewontin 1980, Schindler and Hilborn 2015). While this approach is a component of effective management because individual ecosystems require specific considerations, there remains a critical need to identify general patterns and processes in ecosystems that may create simpler management approaches that account ecosystem complexity and variability.

Ecosystems are subject to an increasing number of anthropogenic stressors that may affect their function and the services they provide (Vitousek *et al.* 1997, Halpern *et al.* 2008). Stressors such as climate change, habitat alteration, land use change, eutrophication, harvest, and population augmentation each impact of species and ecosystems (Halpern *et al.* 2007). Additionally, many stressors interact to affect ecosystems in complex ways (Crain *et al.* 2008, Darling and Cote 2008). These stressors impact ecosystems over a variety of scales, some of which may be outside the direct control of resource management and may require broad-scale policy solutions. Challenges for research and management are to understand these different stressors and their interactions and to identify how ecosystems could respond in the future. Most importantly, we need to identify possible management actions that enable ecosystem resilience to multiple stressors.

Ecosystems provide many different services ranging from provisioning services like fisheries and timber, to regulating services like water purification, to cultural services like wilderness and recreation (Millenium Ecosystem Assessment 2005). Traditionally, management has focused on optimizing the delivery of individual ecosystem services. However, these individual services may interact in ways where deriving one service may negatively impact the delivery of another (Holling and Meffe 1996, Rodriguez *et al.* 2006, Bennett *et al.* 2009). Further, different people place different values on ecosystems and what they provide. Given increasing recognition of potential negative interactions between competing services, there have been increasing emphasis toward implementing ecosystem-based management (Pikitch *et al.* 2004, Hall and Mainprize 2004, Patrick and Link 2015) that incorporates multiple services and stakeholders (Link 2010). In trying to balance multiple objectives and stakeholders, a challenge for ecosystem-based management is identifying where there are likely to be strong interactions between specific ecosystem services and where interactions may be weak. Management can then focus on tailoring management approaches to account for interactions in places where they are particularly strong.

There is increasing recognition that humans and ecosystems are linked in complex social-ecological systems and that changes in either the human or natural component impact the other (Liu *et al.* 2007). Human societies put a variety of pressures on ecosystems, leading to change in populations and in ecosystems (Vitousek *et al.* 1997). Changes in ecosystems in responses to human stressors coupled with substantial natural variability impact ecosystem services that society depends on. Policy and regulations are designed to maintain or improve the flow of resources to people, but they also influence how humans impact ecosystems and cope with their natural variability. Additionally, links been the human and natural components of social-ecological systems operate at local to global scales. These complex links and feedbacks between components make predicting future change difficult. Therefore, we need approaches for creating sustainable social-ecological systems that are robust to uncertainty about the future (Schindler and Hilborn 2015).

In this dissertation, I present four chapters that are each individual case studies that address these challenges for management of multiple stressors influencing populations, balancing multiple objectives and stakeholders, and providing resilience in complex social-ecological systems. In chapter one, I examine how multiple stressors interact to influence the resilience of a commercially important species, sockeye salmon *(Oncorhynchus nerka)*, by impacting important life-history variation. Diversity in life history strategies among individuals makes species resilient to changing environmental conditions (Hutching and Myers 1994, Wilbur and Rudolf 2006) and provides stability to ecosystem services dependent on their populations (Schindler *et al.* 2010). I examined changes in the prevalence of different life history strategies of sockeye salmon returning to Bristol Bay since 1963. I found that while local management for sockeye salmon is highly effective at maintaining abundant populations, larger-scale stressors such as climate change and competition in the ocean are interacting to simplify the age structure present in sockeye salmon populations. While global stressors like climate change may be difficult to change at a local or regional scale, these results suggest that managers may be able to conserve important age class complexity by curtailing stocking of salmon into the North Pacific Ocean. Given the importance of age structure for the reliability of fisheries dependent on sockeye salmon (Hilborn *et al.* 2003, Schindler *et al.* 2010) and for buffering against uncertainty about future changes, management could prioritize approaches that preserve complexity in populations.

In chapter 2, I examine two competing ecosystem services and identify key ecological processes that govern the nature of their interaction. While ecosystems provide many services, different services often compete, resulting in a tradeoff where the delivery of one ecosystem service negatively impacts the delivery of another (Bennett *et al.* 2009). Accounting for such tradeoffs could fundamentally change the way an ecosystem should be managed (Link 2010). Commercial fisheries are typically managed to produce maximum sustainable yield (MSY) of a target species, but reducing the abundance of this species through harvest has impacts on other species and ecosystem function (Pikitch *et al.* 2004, Link 2010). I examined a tradeoff between harvesting sockeye salmon in commercial fisheries versus allowing more to spawn for the benefit resident trout, who rely on their annual energy for their growth and production (Scheuerell *et al.* 2007). This tradeoff also involves multiple stakeholders as resident trout are the foundation of valuable sport fisheries (Duffield *et al.* 2007). I found that density-dependence in sockeye salmon production resulting from competition for space on the spawning grounds results in both MSY for commercial fisheries and most of the growth benefit for trout occurring at similar levels of escapement. Density-dependence, which is present in all populations, is a mechanism that will produce weaker tradeoffs between competing objectives and could be used to identify management priorities for ecosystem-based management. Because density-dependence is ubiquitous, we need to change our default assumptions about tradeoffs between services that are dependent on the changing abundance of species.

In chapter three, I examined how sockeye salmon use available spawning habitat under varying population abundance. Habitat selection plays an important role in population regulation, predator-prey interactions (Rodenhouse *et al.* 1997), and may influence the efficacy of habitat restoration strategies. By examining how sockeye salmon distribute among available habitat patches as their population abundance varies by more than an order of magnitude, I show that habitat use changes under increased population abundance as individuals spawn in suboptimal habitats, presumably to avoid high conspecific interference. The degree of this change is dependent on the availability of high quality habitat patches, which is controlled by local habitat characteristics. These results have important consequences for the tradeoff discussed above because habitat selection affects the availability of salmon eggs for stream consumers at a given escapement and this effect will depend upon the underlying habitat characteristics of the stream. This also has implications for determining the effectiveness of habitat restoration projects, as populations may only use restored habitats if abundance is high enough to force them to use it. Alternatively, if the restored habitat is now the best habitat, individuals may switch habitats. Therefore, increases in abundance at a restored reach may not indicate increases in total abundance. Considering different constraints on how individuals select and use habitats, both habitat quality and competition, is important for managing and restoring species.

In my final chapter, I examined two strategies that may be used to buffer human communities against uncertainty in the future conditions of social-ecological systems. Fishing is an important livelihood source for millions of people globally (Adger 2000). Fisheries are affected not only by biological responses in species to oceanographic changes, but also by policy, socio-economic conditions, and market demand (Clark 1981). Therefore, people that depend on fisheries for food and their livelihood need to be able integrate over variability in the aggregate social-ecological system (Allison and Ellis 2001). In this chapter, I examined whether diversification and turnover of fishing opportunities buffered Alaskan fishing communities against large-scale changes in both ocean productivity and natural resource markets. I found that fishing communities that participated in a more diverse set of fisheries were more buffered against unexpected shifts in the social-ecological system. Additionally, more diversified communities were better able to adapt to changing conditions by switching among fishing opportunities. Providing communities with options and encouraging diversification are tangible strategies for enabling resilient communities in the face of irreducible uncertainty about future change and to buffer society from unexpected shifts in ecosystem services.

Maintaining ecosystem services given considerable uncertainty about the future will always be challenging and require significant research and effort moving forward. Understanding the increasing number of stressors that are affecting ecosystems, balancing the needs of different stakeholders, understanding the effectiveness of habitat restoration, and integrating management of humans as part of complex social-ecological systems will continue to complicate management. Ecosystems are complex and we often try to manage all of that complexity. As a whole this research demonstrates that this natural complexity may actually alleviate some of these challenges for managing ecosystems for the future. In this dissertation, I showed how several common patterns and processes that enable resilience in ecosystem services for people and mechanisms that can be exploited to make management with uncertain global change simpler.

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Chapter 1. Effects of global change on the complex life cycle of an exploited species

1.1 ABSTRACT

Diversity in life history strategies among individuals makes species resilient to changing environmental conditions and adaptable to new opportunities and constraints on their population dynamics. Global change is likely to generate unexpected responses in life histories because of complexities between habitat-specific effects on certain life stages, and developmental linkages as individuals complete their life cycles. The life histories of exploited fish species, such as Pacific salmon, are vulnerable to a wide variety of anthropogenic stressors including climate change, selective exploitation, and competition with hatchery releases for finite foraging resources. We used multivariate time-series models to quantify changes in the life history characteristics of sockeye salmon from Bristol Bay, Alaska, over the last half century, focusing on how they partition their lives between freshwater habitats and the ocean. Climate warming has decreased the time salmon spend in their natal freshwater habitat, presumably in response to climate-enhanced growth opportunity. In the ocean, increased competition with hatchery releases, and that fish migrate from freshwater at a younger age, have delayed maturation toward spending an additional year feeding in the ocean. Effects of size-selective fishing were negligible. These stressors combined to decrease the size-at-age of fish vulnerable to commercial fisheries and have the potential to erode the age class complexity that stabilizes this highly reliable resource.

1.2 INTRODUCTION

Species with complex life cycles, i.e. including those that involve migrations between different habitats to complete their life cycles, may be particularly sensitive to global change because each life stage is influenced by a unique set of natural and anthropogenic stressors specific to the different habitats a species exploits throughout its life cycle (Kingsolver *et al.* 2011, Salice *et al.* 2011). Individual life stages differ in their sensitivity to individual stressors, particularly temperature (e.g., Pörtner & Farrell 2008, Radchuk *et al.* 2013). Additionally, the effects of environmental change experienced by a population in one habitat affect their ecology in other life stages through developmental linkages in the process of completing life cycles. While responses can be measured for individual life stages, the integrated response of a population to multiple stressors may be different than the sum of the components (Folt *et al.* 1999). Understanding how multiple natural and human stressors interact within and among life stages to influence life history traits and population level processes is critical for informed management of resources into the future.

Global change involves a complex mix of forces, including climate change, eutrophication, exploitation, habitat degradation, invasive species, and hatchery production (Vitousek *et al.*1997, Halpern *et al.* 2008). These human-driven stressors are occurring among large-scale climate phenomena and population and community dynamics that together produce complex ecological responses. A major focus of research has been the complexities of how stressors act over different life stages (Kingsolver *et al.* 2011, Radchuk *et al.* 2013), space and time (Webster *et al.* 2002), and the interactive potential of stressors (Crain *et al.* 2008, Darling and Cote 2008, Hodgson *et al.* 2017). The multi-dimensional and interactive effects of global change make detecting and understanding its effects on life cycles of organisms, particularly elusive.

Life history traits and the diversity expressed within species are essential components of populations and ecosystems (Hutching and Myers 1994, Wilbur and Rudolf 2006, Hilborn *et al.* 2003). Life history traits such as hatch timing, migration timing, and ontogenetic shifts are adapted to local ecological conditions. Diverse life history strategies, such as staggered age structure, reduce the risk of an entire cohort encountering unfavorable environmental conditions (Hutching and Myers 1994, Wilbur and Rudolf 2006) and allows for adaptation to environmental change. Shifts in the life history strategies present in populations affect their productivity as well as responses to stressors (Rouyer *et al.* 2011). Changes in life history traits are of key importance for conservation and management, but responses of ecologically and economically important species remain largely unknown, particularly for species that involve complex life histories.

Human and natural selective pressures have altered the life history characteristics of many species (Palumbi 2001, Darimont *et al.* 2015, Ohlberger *et al.* 2011). Fishing is widely known to affect life history traits of populations by selecting against older larger individuals moving toward younger, smaller, and more quickly maturing individuals (Olsen *et al.* 2004, Kuparinen and Merilä 2007, see exception Biro and Post 2009). Climate change is indirectly imparting selective pressures on species by altering food availability, growth potential, and changing key life history timing events such as spawning and emergence (Bradshaw and Holzapfel 2006, Hoffman and Sgro 2011, Edwards and Richardson 2004). Hatchery augmentation is a common practice in many commercially valuable fish stocks, despite mounting evidence of important ecological interactions with wild populations (Araki *et al.* 2007, Ruggerone *et al.* 2003, Amoroso *et al.* 2017). Within a single species, populations integrate across multiple stressors yielding diverse responses over time.

Pacific salmon (*Oncorhynchus* spp.) are ecologically, economically, and culturally valuable for people living around the North Pacific rim. Populations of Pacific salmon are found throughout the Pacific rim stretching from Japan to the United States, forming the basis of commercial, sport, and subsistence fisheries. Pacific salmon have a complex life cycle dependent upon both freshwater and marine habitats. Juvenile salmon hatch and rear in rivers, streams, and lakes before migrating to the ocean as smolts where they attain most of their growth. Adult salmon then return to their natal freshwater habitat to spawn. Their broad geographic range and long distance migrations coupled with their complex life cycle render salmon populations vulnerable to a diverse set of stressors expressed at both local and global scales.

Pacific salmon are increasingly subjected to a wide range of human and natural stressors such as harvest, modifications to freshwater and estuarine habitats, hatchery practices, and changing climate conditions. Habitat alteration and hatchery practices have had substantial impacts on many stocks (Nehlsen *et al.* 1991, Araki *et al.* 2007). Even in places where habitat is largely intact, and salmon stocks are highly productive, populations are still vulnerable to a suite of stressors acting across life history stages. Effective conservation of salmon populations and continued sustainable harvest will require understanding how these stressors interact to affect population structure and productivity (Karieva *et al.* 2000).

We quantified changes in life history traits of sockeye salmon returning to Bristol Bay Alaska since 1963. Bristol Bay, located in southwest Alaska, is one of the most productive salmon producing regions globally. An average of 37.5 million sockeye salmon over the last 25 years return to spawn in rivers in this region, supporting fisheries that harvest half of the global catch of sockeye salmon (EPA 2014). With age composition data from sockeye returning to seven major rivers systems in Bristol Bay, we test how rapid climate warming, ocean conditions, and competition in freshwater and the ocean, and fishery exploitation are influencing the duration of freshwater residency and age at maturity in the ocean – two critical life history transitions for this species. We applied multivariate time series analysis to include spatial coherence between populations while testing for the influence of these human and natural drivers. We show that there have been significant shifts in both the freshwater and ocean life history stages. These trends in life history traits are most strongly the result of climate warming and competition with hatchery-released salmon in the ocean. Additionally, the changes in freshwater strategy are linked to the age at maturation in the ocean.

1.3 RESULTS

There have been clear shifts in the age composition of sockeye salmon returning to Bristol Bay since brood year 1963 (Figure 1.1), yet, the average age (freshwater + ocean) has not changed (generalized least squares, P=0.31). Rivers across the stock complex differ in their freshwater and ocean age compositions, likely reflecting differences in spawning and rearing conditions encountered in different rivers (Quinn *et al.* 2009). But, many systems have seen increases in the proportions of younger freshwater ages and increases in the 1.3 age class (Figure 1.1). While the observed changes in age composition at Bristol Bay scale appear to have similar patterns to some of the systems, changes in age at the aggregate Bristol Bay are subject to the major changes in the productivity of these rivers with characteristic age groups. To circumvent this issue, we applied a multivariate time-series technique to quantify common trends in age composition that are shared across seven of the major river systems. We decomposed the salmon life cycle into freshwater and ocean components and searched for common patterns in each. Additionally, we test for the influence of environmental covariates that might affect the freshwater residency or age at maturation.

Since 1950, there have been changes in both freshwater and ocean environmental conditions, which have the potential to influence life-history transitions in sockeye salmon (Figure 1.2 A,B). Southwest Alaska has been warming rapidly. Spring ice breakup dates on sockeye salmon nursery lakes in Bristol Bay have occurred significantly earlier, and summer lake temperatures have increased. Ice breakup on Lake Aleknagik, a major lake in the Wood River system, has occurred on average 2.5 days/decade earlier (GLS, $p < 0.01$) and summer lake temperatures have increased by 0.5ºC/decade (GLS, $p = 0.04$), both leading to longer and more productive growing seasons (Figure 1.2 A). Earlier ice off, and warmer lake conditions are positively correlated with *Daphnia spp.* densities, a primary food source for juvenile sockeye (Schindler *et al.* 2005, Carter *et al.* 2012) and juvenile salmon growth (Rich *et al.* 2009). In the North Pacific Ocean, the primary rearing area for sockeye, there have been changes in surface temperature as well as upwelling and productivity. Pacific Decadal Oscillation (PDO) is an interdecadal shift in sea surface temperature and is strongly correlated with sockeye productivity in Alaska (Mantua *et al.* 1997). A pronounced warm phase of the PDO, with well-described positive effects on sockeye salmon populations in Alaska, began around 1977 and persisted for more than 20 years (Figure 1.2 B). North Pacific Gyre Oscillation (NPGO) is correlated with primary productivity in the Gulf of Alaska and is correlated to sockeye productivity (DiLorenzo *et al.* 2008). We examined the potential influence of these environmental changes on the age composition of sockeye salmon returning to Bristol Bay.

To evaluate changes in life history transitions for sockeye salmon, we applied a multivariate autoregressive time series approach, dynamic factor analysis (DFA, Zuur *et al.* 2003) to age composition time series from seven major river systems in Bristol Bay. DFA is a dimension reduction technique similar to principal component analysis developed for use with time series. DFA searches for shared trends among many time series and can include important covariates driving dynamics in each of the time series.

To evaluate changes in the duration of freshwater residency of Bristol Bay sockeye salmon we searched for common trends in time series of the proportion of fish spending only one year in freshwater across seven Bristol Bay rivers. There was a clear effect of lake conditions on the proportion of sockeye salmon spending only one year in freshwater (Figure 1.3 A) with an increasing proportion of age-1 smolts and a decline in age-2 smolts since 1963 (Figure 1.3 B). Therefore we evaluated DFA models that included an environmental covariate such as ice out, lake temperature, PDO, and NPGO. Additionally, increased competition from high densities of juvenile sockeye in the rearing lakes in an ecosystem may increase the duration of freshwater residency, so we tested models that included environmental covariates and the number of spawning adults as a proxy for juvenile density. A full model selection table is provided in Supplementary Table 1. This trend towards increasing proportions of age-1 smolts is due to both lake temperature and an additional positive latent trend. Lake temperature was positively correlated with this strategy of shorter freshwater residency and was quite strong across all systems (effect sizes > 0.3, Figure 1.3 C). Support for density dependence in freshwater as an influence on age composition was weak (Supplementary Table 1). This is likely due to a lack of strong contrast in the number of spawning salmon (used as a proxy of juvenile abundance and competition) as a result of accurate management for escapement goals. There was an additional positive residual trend in the proportion of sockeye only spending one year in freshwater that was consistent across all systems including those that have historically been dominated by sockeye spending one year in freshwater (Figure 1.3 D). This trend reflects shared variation that is not explained by factors we considered or have data to characterize. Overall, climate warming in this region has substantially reduced the prevalence of sockeye spending two years in freshwater. These changes could influence the overall age at maturation, diversity and productivity of these stocks.

To evaluate changes in the ocean residency and age at maturation we applied DFA to time series of the proportion of sockeye spending three years in the ocean across the seven Bristol Bay rivers (nearly all fish spend either 2 or 3 years in the ocean). There was a strong positive relationship between the freshwater life history strategy and years spent in the ocean (Figure 1.4 A). Therefore we assessed models including the proportion spending only one year in freshwater as a covariate. We also tested the ocean climate indices, PDO and NPGO (Figure 1.2 B) in the first two years of ocean residency as covariates.

Overall, there was a strong increase in the proportion of sockeye spending three years in the ocean (Figure 1.4 B) with a commensurate decline in the proportion spending only 2 years in the ocean. This trend toward longer ocean residency was described by shorter freshwater residency (Figure 1.4 C) and a residual latent trend (Figure 1.4 D). Overall, the average increase in the proportion of ocean age three across systems was 0.3 (range 0.11-0.45), and the influence of changes in freshwater life history strategy increased the proportion by an average of 0.18 (range 0.09-0.36).

As with the freshwater life history stage, competition for resources has the potential to influence ocean age at maturation. The residual positive trend in the proportion of sockeye returning after three years in the ocean was highly correlated (Pearson correlation = 0.98) with the number of juvenile pink and chum salmon (95% of all non-Chinook hatchery produced juvenile salmon) released from hatcheries across the North Pacific Ocean (Figure 1.4 E). Hatchery influences increased the proportion of sockeye spending three years an average of 0.12 (range 0.02-0.31), or about 40% of the total change. Hatchery released pink and chum salmon constitute the vast majority of hatchery-released salmon and have potential to compete with sockeye salmon due to high dietary and spatial overlap with sockeye salmon (Johnson and Schindler 2009, Myers *et al.* 1996). This mechanism of reduced growth rates due to increased competition in the ocean is supported by a negative relationship between North Pacific hatchery releases and the average weight of sockeye returning to Bristol Bay fisheries after two years in the ocean (Figure 1.4 E). Size in their second year in the ocean affects the decision to mature and return after two years in the ocean or to stay in the ocean for three or more years (Morita and Fukuwaka 2006). There was no statistical support for the influence of ocean climate indices on ocean age (Supplementary Table 2); however, there was a clear signal of competition for resources playing out at the scale of the North Pacific Ocean in the ages at maturation of wild sockeye salmon. This has important consequences for wild salmon stocks and provides clear evidence of negative impacts of hatchery augmentation on wild stocks, particularly with the interaction with ongoing climate change. A hatchery-climate interaction can be expected in the ocean as the quantity of thermal habitat for salmon in the North Pacific is expected to decrease in the future (Schindler *et al.* 2008, Abdul-Aziz *et al.* 2011).

Fishery selection also has the potential to change the age at maturation of sockeye salmon, as gillnets used in this fishery are size-selective (Kendall *et al.* 2009). We tested DFA models for changes in age at maturation that included fishing district specific exploitation rates lagged by zero, one, and two generations. We found no influence of up to two generations of fishery exploitation on the patterns of ocean age composition observed in this study (Supplementary Table 3). Additionally, the expected direction of selection would favor the return of salmon only spending two years in the ocean as they are less susceptible to gill nets used in this fishery (Kendall *et al.* 2009), the opposite response to the trend we describe.

1.4 DISCUSSION

Over the last five decades, there have been substantial shifts in the age composition of Bristol Bay sockeye, and these changes are coherent across the seven major river systems of this region. The proportion of sockeye spending only one year in freshwater has increased as lakes have warmed and become more productive. Changes in freshwater age, and its influence on the ecology of salmon in the ocean, along with increased competition in the ocean have delayed maturation and increased the proportion of sockeye spending three years in the ocean before returning to spawn in rivers. These changes in life history traits for sockeye salmon have the potential to influence age diversity, population productivity, and fish size, all of which have implications for a highly valuable and reliable commercial fishery.

Climate change is having clear impacts on the early life history of sockeye salmon. Warmer lake temperatures in this system are correlated with shorter freshwater residence. This trend is likely due to improved growing conditions. Longer ice-free seasons and warmer lake conditions are increasing food availability and growing season length (Schindler *et al.* 2005, Carter *et al.* 2012). Changes in early life history can influence sockeye salmon population productivity as the first year in freshwater and the first year in the ocean are two life stages during which enormous mortality occurs (Smith 2000). Improved environmental conditions may be improving the condition of juvenile salmon as they leave freshwater, but the influence of changes in life history from two freshwater years to one year on changes in survival in the ocean needs further evaluation. However, these changes in freshwater residency are spilling over to influence the ecology of sockeye in their ocean life history stage and ultimately altering their maturation schedules.

Changes in age at maturation in Bristol Bay sockeye salmon are driven by changes in the freshwater life history strategy and increased competition from hatchery released pink and chum salmon in the ocean. We found that increased competition has slowed growth as indicated by a strong correlation between stocking rates of hatchery salmon at the scale of the North Pacific and size-at-age for Bristol Bay sockeye spending two years in the ocean. The evidence for overcrowding of salmon in the ocean and increased competition for resources has been gaining strength (Ruggerone *et al.* 2003, Ruggerone *et al.* 2015). Hatchery production has increased substantially since 1970, and there is high spatial and trophic overlap between sockeye, pink, and chum salmon in the North Pacific (Johnson and Schindler 2009, Myers *et al.* 1996). Growth and survival in North American salmon stocks have been shown to be negatively affected by hatchery-produced pink salmon (Ruggerone *et al.* 2003). Fraser River, British Columbia, sockeye salmon length-at-age and age-at-maturity are also influenced by the abundance of salmon in the North Pacific (Ruggerone and Conners 2015). Fewer fish are likely reaching a threshold size to return and are instead opting to spend an additional year in the ocean. Thus the change in the proportion of sockeye spending three years in the ocean is strongly correlated to pink and chum salmon hatchery releases. A challenge for management is that hatchery production is not subject to all of the natural negative feedbacks, such as density dependence during spawning and rearing, which limit population productivity of wild stocks. Additionally, identifying ocean scale competition is challenging. Nevertheless, continued augmentation of salmon stocks may undermine the complexity that enables thriving wild salmon populations.

Changes in size and age of marine fishes have been linked to selection by commercial fisheries (Sharpe and Hendry 2009, Darimont *et al*. 2009). Previous research on the Bristol Bay fishery has suggested that gillnet selection in Bristol Bay sockeye has reduced size-at-age (Kendall *et al.* 2009, Kendall *et al.* 2014), shifting sockeye toward smaller and younger fish. Directional selection against larger individuals could influence maturation timing and ocean residency. However, we found no evidence that fishery exploitation influenced the changes in age at maturation observed in this study (Supplementary Table 3). We found an increase in the proportion of salmon spending three years in the ocean, the opposite of the expected direction for fisheries selection. Importantly, the changes in ocean age due to competition are plastic responses to environmental influence not genetic responses to selection and harvest practices, and therefore should have shorter time horizons for reversal.

Diversity in age composition plays a strong role in reducing variability in salmon runs with importance for fishers, communities, and industry which rely on annual salmon returns (Schindler *et al.* 2010). In Bristol Bay, age structure alone reduces year-to-year variability in runs to Bristol Bay by 50% compared to if runs were of a single age (Schindler *et al.* 2010). Continuing trends toward shorter freshwater residency and delayed ocean maturation could translate into simplification of age structure and reduced stability. Increases in the proportion of salmon only spending one year in freshwater and competition in the ocean are favoring the 1.3 life history type, which has increased in all systems. This trend has led to a simplification of age structure in several of the systems (Figure 1.1). In the two systems where this age class was historically a small proportion, Kvichak and Egegik, the changes in life-history traits have increased diversity among age classes (Figure 1.1). However, ongoing climate change should further increase lake temperatures, which will likely continue moving all systems towards being dominated by smolts that have spent a single year growing in freshwater habitat. The combined effect of climate on the freshwater life history and its importance for ocean residency and maturation should change the age composition for all systems towards a simplified age structure consisting of a majority of 1.3. Simplification of age structure favors cohort resonance (White *et al.* 2014), volatile recruitment, and other systematic drivers of variation in abundance. Increased run variability would have consequences for the stability of fisheries and other ecosystems services provided by these ecosystems. Maintaining diversity in age structure is an important component of sustaining stable populations in the face of various anthropogenic and natural stressors and should be a goal for conservation.

Humans are rapidly changing many of the key drivers for species and ecosystems with potential consequences for ecosystem services. Impacts from multiple stressors not only have impacts on population productivity (Crain *et al.* 2008), but as shown in this study, these drivers are altering life-history strategies. Importantly, changes in one life stage carry over and influence strategies selected in later life stages having potential consequences for population variability and stability of ecosystem services. Understanding the potential influences of multiple stressors and their interactions on life-history diversity is important for the conservation of populations and ecosystems in the future.

1.5 METHODS

Study System

Bristol Bay, located in southwest Alaska, has nine major rivers systems, which have diverse freshwater environments. Spawning and rearing habitats range from small streams to large lakes, and each integrate climate, density dependent effects, and fishing pressure differently. In turn these systems support different life history strategies. This translates into variability in age and size across the region. Together these rivers support a large population of sockeye salmon. These returns support a highly valuable commercial salmon fishery that targets primarily sockeye salmon at the mouths of these rivers. Commercial fishing operates in five fishing districts, some exploiting multiple rivers, using exclusively gill nets. Fisheries harvests over this same period have averaged about 70% of the total return or 24 million fish (Alaska Department of Fish and Game).

Data

Sockeye salmon age, sex, and size information has been collected by the Alaska Department of Fish and Game since the late 1950's. Data is collected both from fish captured in commercial fisheries and from those that have passed through the fishery. Run size and age data from commercial harvests are partitioned to individual river systems using genetic and age class information (Cunningham *et al.* 2017). We use age data from seven of the nine river systems in Bristol Bay (Figure 1.1). We do not use data from Togiak and Nushagak river systems because they have large populations of river-type sockeye that have different characteristic age classes. Age in these systems can change rapidly over time due to differing productivity of river versus lake type sockeye. In the remaining seven rivers, greater than 95% of all sockeye belong to one of four age groups, 1.2, 1.3, 2.2, and 2.3. For model analysis we separated the life history into freshwater and ocean phases. This allowed one time series from each system representing the freshwater phase and one time series for the ocean phase. We use proportional data due to highly variable run sizes over time within each of the river systems. These data were normalized using the logit transformation.

We tested the effects of several climate covariates and juvenile competition on the freshwater age of sockeye salmon. Freshwater covariates have been collected by the University of Washington's Alaska Salmon Program since the 1950's. Ice off date and lake temperature come from Lake Aleknagik in the Wood River system. Lake temperature is the average June, July, and August temperatures from the top 20 meters, measured biweekly. Freshwater covariates were lagged to align with the first summer spent in freshwater (Brood year + 1). We assumed that interannual variation in thermal conditions observed in Lake Aleknagik were indicative of general climate patterns observed over the region. We also tested two ocean climate indices known to influence sockeye salmon production and regional freshwater climate conditions, Pacific Decadal Oscillation (PDO; Mantua *et al.* 1997) and North Pacific Gyre Oscillation (NPGO; Di Lorenzo *et al.* 2008). Both indices are available online (http://research.jisao.washington.edu/pdo/, http://www.o3d.org/npgo/). Density effects in the freshwater life stage were estimated using the escapement to each river system as an index of juvenile production and competition for each brood year (Schindler *et al.* 2005).

We tested for climate influences, density effects, and fishery selection on the ocean age of sockeye salmon returning to Bristol Bay. We used a four-year moving average of ocean indices PDO and NPGO for each brood year that aligns with the first and second years in the ocean for sockeye leaving the ocean after one and two years in the freshwater. There is a positive relationship between the freshwater life history stage and duration of ocean residency (Figure 1.3). We evaluated models that included system specific proportions of sockeye spending only one year in freshwater. We used pink and chum hatchery releases as an index of competition in the ocean, because these species constitute the majority of young salmon in the ocean and have a large diet overlap with sockeye (Johnson and Schindler 2009). Changes in total Pacific salmon abundance are highly correlated with hatchery releases (Supplementary Figure 1). Data on total salmon abundance and hatchery releases are available from the North Pacific Anadromous Fish Commission (www.npafc.org).

To test for the influence of fishery selection we evaluated models including system specific exploitation rates. We tested for fishery selection from exploitation rates lagged by zero, one, and two generations.

Analytical approaches

To search for common trends in freshwater age and ocean age (separate analyses) among the seven different river systems as well as test for the influence of covariates we used dynamic factor analysis (DFA; Zuur *et al.* 2003). Similar to principal component analysis, DFA is a dimension reduction technique designed specifically for use with time series data. With DFA, we are trying to explain temporal variation in a set of *n* observed time series using linear combinations of independent hidden random walks and covariates. The model structure is as follows:

The state equation of a vector of common random walk trends over time:

$$\boldsymbol{x}_t = \boldsymbol{x}_{t-1} + \boldsymbol{w}_t \qquad \boldsymbol{w}_t \sim MVN(0, \boldsymbol{Q}) \tag{1}$$

Observation equation relates trend ($\boldsymbol{x}$) to observations ($\boldsymbol{y}$).

$$\boldsymbol{y}_t = \boldsymbol{Z}\boldsymbol{x}_t + \boldsymbol{D}\boldsymbol{d}_t + \boldsymbol{v}_t \qquad \boldsymbol{v}_t \sim MVN(0, \boldsymbol{R}) \tag{2}$$

Here, the vector of observations for proportion freshwater-1 (or proportion ocean-3) at time t ($\boldsymbol{y}_t$) are modeled as linear combinations of hidden trend ($\boldsymbol{x}_t$) and factor loadings on the hidden trend for each river ($\boldsymbol{Z}$) as well as any included covariates ($\mathbf{d}_\mathbf{t}$) and their associated coefficients (**D**). $\boldsymbol{v}_t$ and $\boldsymbol{w}_t$ represent the observation and process error structures respectively. To make the model estimable (Zuur *et al.* 2003) process error ($\mathbf{Q}$) was set to a diagonal matrix of value 1. Observation errors (**R**) are from a multivariate normal distribution. Model structure including covariate combinations are determined through model selection. Candidate models were compared using AIC based on the maximum likelihood of the model fit. Model selection results for DFA analyses are in Supplementary Tables 1, 2, 3.

We compared models with one latent trend as well as an unconstrained error structure, and also included different combinations of covariates. Unconstrained error structure allows all rivers to have individual observation errors as well as pair-wise covariance. We tested alternate error structures where all rivers share a single observation error (diagonal and equal) and where all rivers have individual observation error (diagonal and unequal), but unconstrained models vastly outperformed other error structures and therefore we only included unconstrained models in this paper. All data and covariates were z-scored to account for differences in means and intrinsic variance dynamics, and eliminate weighting based on the numerical dominance of some systems. DFA models were fit using a model written in Template Model Builder (TMB) by TJC. Model code was validated using simulated data and accurately recovered ‘true’ parameters used to generate simulated data.

To assess general changes in age composition for Figure 1.1, we applied a Kalman filter smoother to salmon returns to each system prior to calculating proportions (Harvey *et al.* 1989). We also applied a Kalman filter smoother to the sockeye salmon weight presented in Figure 1.4 in order to more easily visually assess trends in the data.

We assessed the strength of trends for date of spring ice breakup and summer lake temperature (Figure 1.2) were determined using generalized least squares regression accounting for autocorrelation at lag-1 (Cowpertwait and Metcalfe 2009).

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1.7 FIGURES

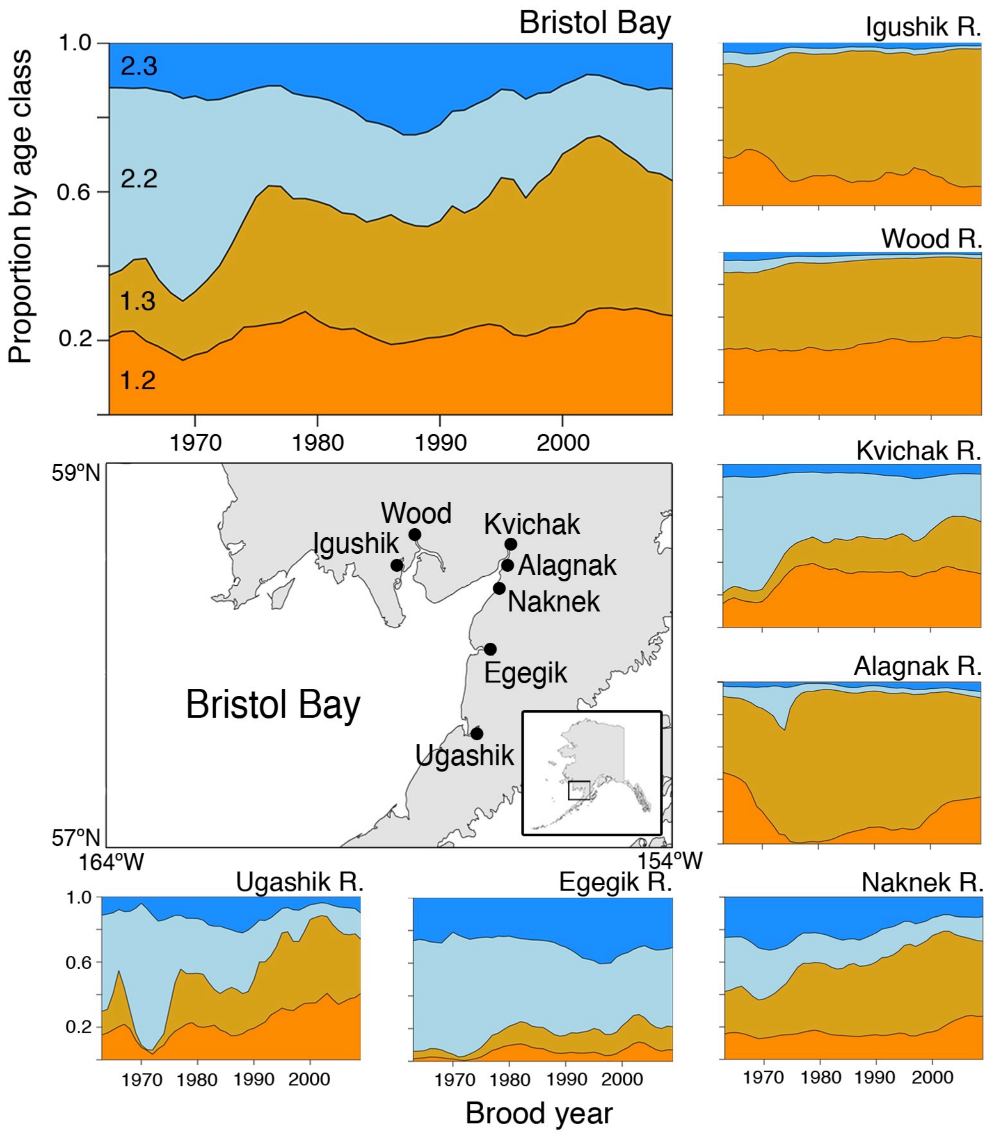

Figure 1.1: Long term age composition of sockeye salmon from seven of the major river systems draining into Bristol Bay, Alaska. Each panel displays the age composition of a river system (or Bristol Bay in aggregate) among the four dominant age classes. Proportions are calculated from returning salmon by age classes that were Kalman filtered prior to computing proportions. Aging convention is freshwater years.ocean years (e.g., 1.2 denotes a fish that has reared for one year in freshwater and two years in the ocean before reaching maturity).

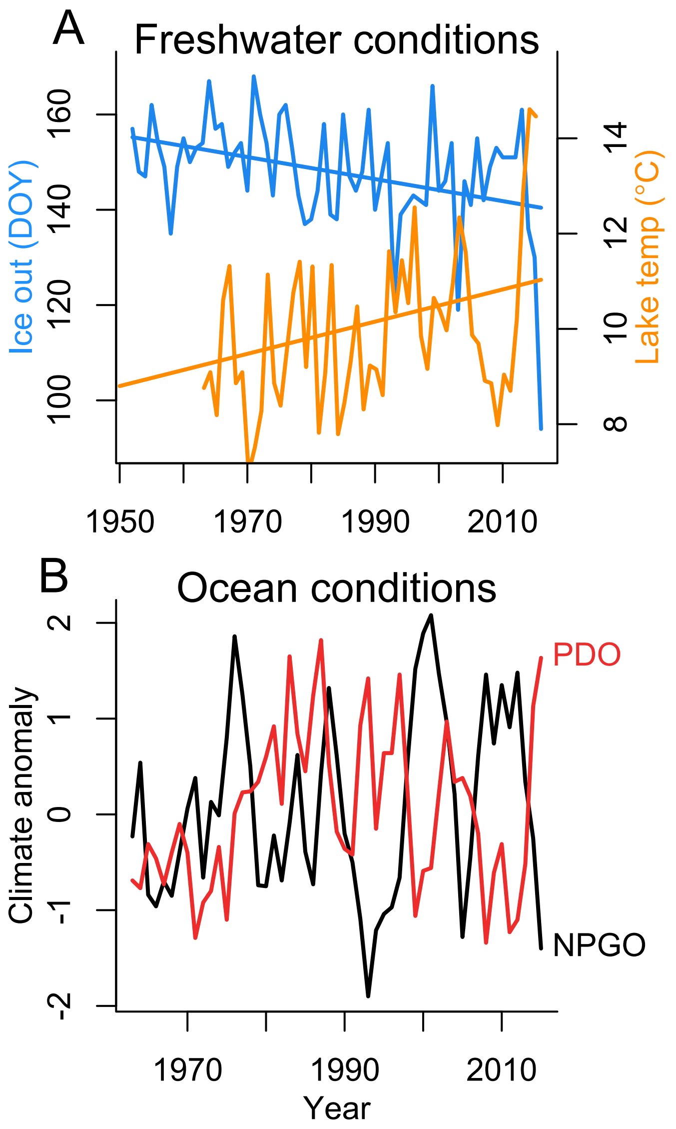

Figure 1.2: Environmental changes in freshwater and ocean habitats for Bristol Bay sockeye salmon. A) Spring ice breakup day of year and average summer lake temperature from Lake Aleknagik, a sockeye salmon rearing lake. Each time series include the generalized least squares fit including temporal autocorrelation. B) Two ocean climate indices known to influence salmon production (PDO=Pacific Decadal Oscillation; NPGO=North Pacific Gyre Oscillation).

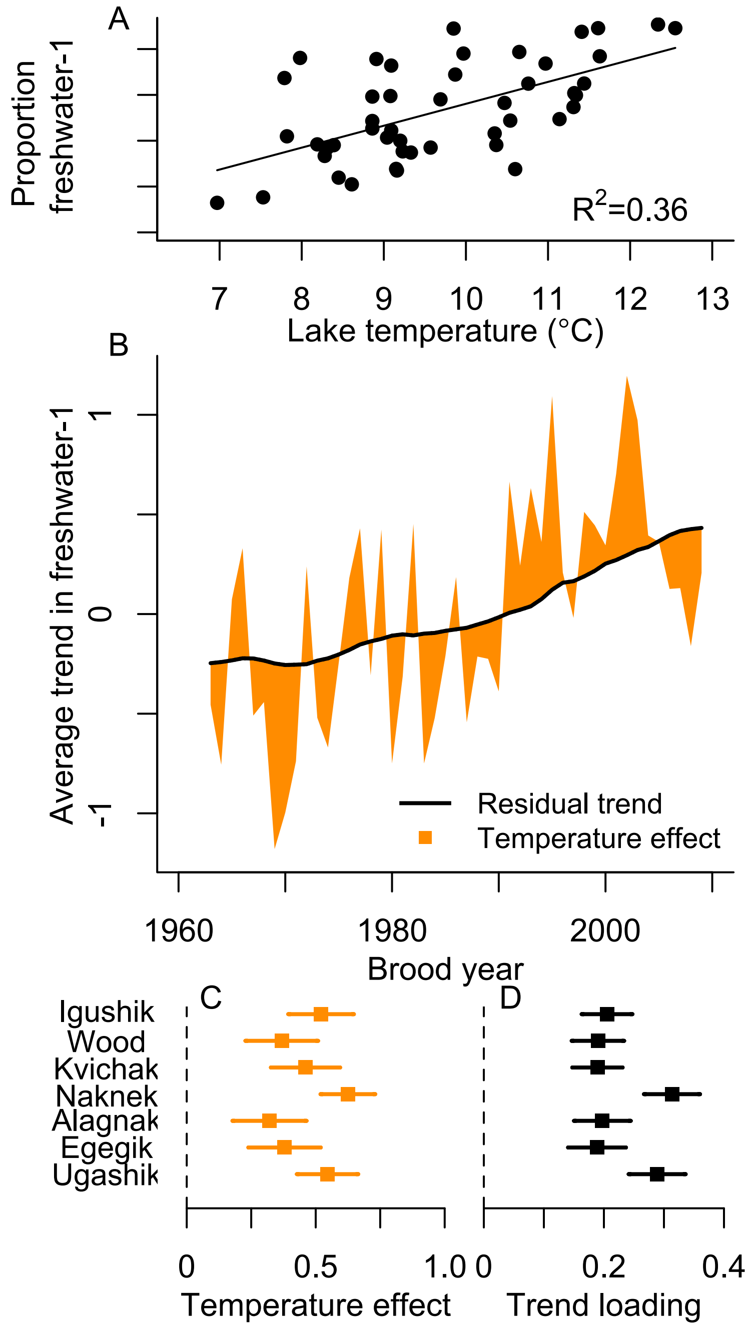

Figure 1.3. Changes in the duration of freshwater residency of sockeye salmon A) Rearing lake temperature plotted against the proportion of Bristol Bay sockeye only spending one year in freshwater. Black line is the least squares line of best fit. B) Average trend and influence of lake temperature on the proportion of sockeye salmon migrating to the ocean after only 1 year in freshwater, as determined by dynamic factor analysis (Supplementary Table 1). The orange

polygons represent the average influence of lake temperature across stocks while the black line is the remaining trend. C) The effect size of lake temperature on the duration of time spent in freshwater across the seven rivers. The orange lines are parameter standard errors. D) The loadings on the residual trend across the seven rivers. The black lines are parameter standard errors.

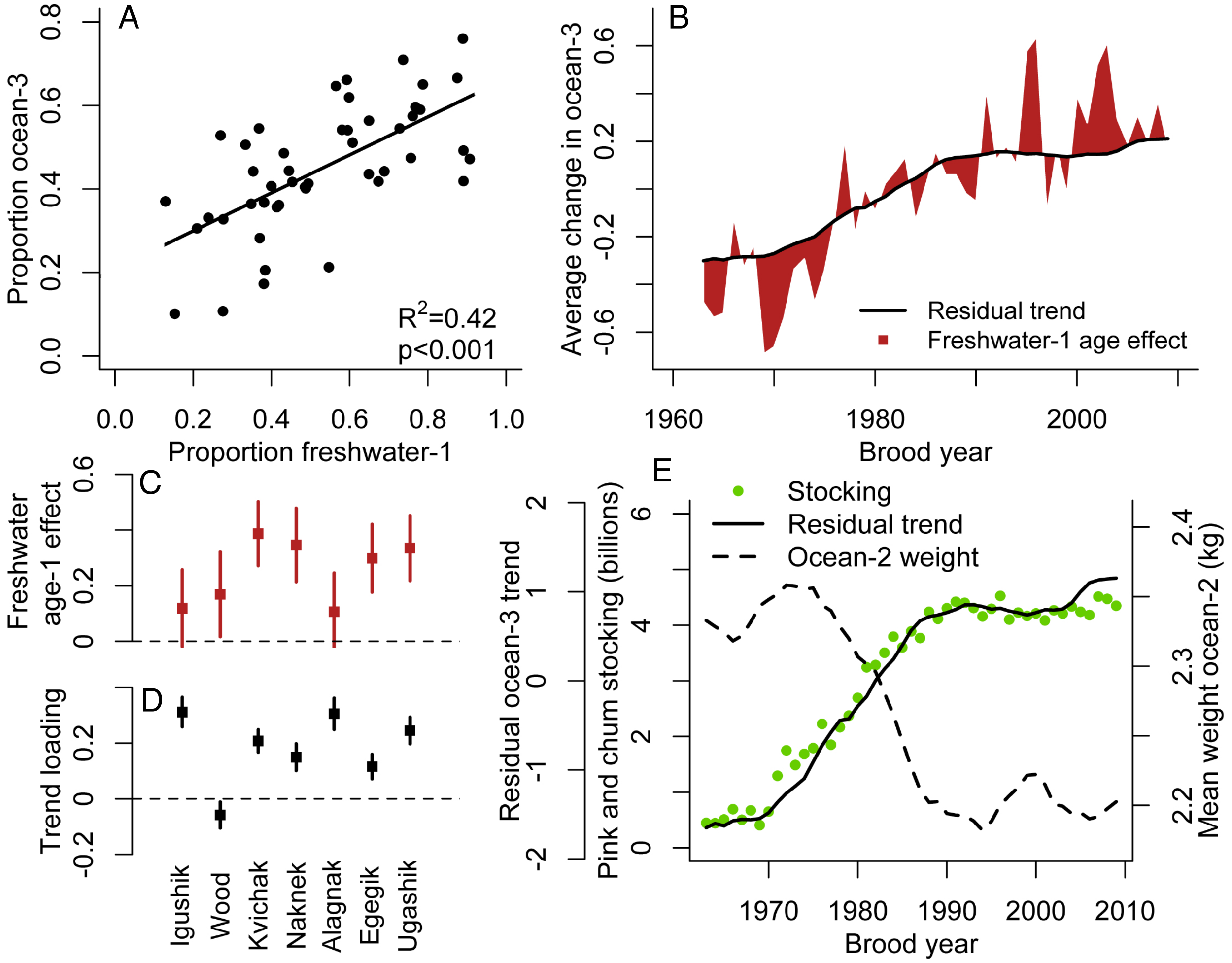

Figure 1.4. Changes in the age at maturation of sockeye salmon A) The influence of the amount of time spent in freshwater on the ocean occupancy as aggregate across Bristol Bay. B) Average trend and influence of duration in freshwater on the proportion of sockeye salmon spending three years in the ocean, as determined by dynamic factor analysis (Supplementary Table 2). The red polygons represent the average influence of duration in freshwater across stocks while the black line is the remaining trend. C) The effect size of duration in freshwater on the duration of time spent in freshwater across the seven rivers. The red lines are parameter standard errors. D) The loadings on the residual trend across the seven rivers. The orange lines are parameter standard errors. E) Residual trend in proportion of sockeye salmon spending three years in the ocean, pink

and chum salmon hatchery releases, and average weight of ocean-2 sockeye salmon returning to Bristol Bay. Average weight is a Kalman filter smoothed time-series of the average weight of ocean-2 sockeye harvested in Bristol Bay.

Chapter 2. Density-dependence and scale mismatch shape ecosystem service tradeoffs

2.1 ABSTRACT

Managing for multiple ecosystem services may require tradeoffs by reducing delivery of one service in order to increase supply from another. Identifying and evaluating important tradeoffs are essential for achieving better ecosystem management and conservation objectives. However, the consequences of alternative management strategies can be obscured by complex ecological interactions that involve nonlinear relationships (e.g., density-dependence), mismatches between the scale of ecological studies and that of management, and uncertainty in both the underlying process and observations. Here, we explore the important relationships that shape the interactions between two competing ecosystem services using a tradeoff between Pacific salmon fisheries and the benefits to resident trout species in the freshwater ecosystems that salmon spawn in. We inform our analysis with empirical datasets on both sockeye salmon populations and resident trout growth from freshwater streams where salmon subsidies form the base of the food web. Ecological constraints imposed by the availability of salmon spawning habitat induce density-dependence on sockeye salmon productivity and the availability of salmon resources for resident trout, creating a complex tradeoff between these two ecosystem services. Population stochasticity at the ecosystem scale creates variation in spawning salmon distributions among habitats within any management target. This provides similar growth for resident trout at the watershed scale across a wide range of management targets, including the targets currently used in a single objective management framework. The same density-dependent mechanism that influences maximum sustainable yield (MSY) in sockeye salmon populations also controls

subsidies for resident trout. Nonlinear ecological dynamics, like density-dependence may be difficult to detect, but fundamentally change the shape of ecosystem service tradeoffs. Due to their prevalence, density-dependence and mismatches in scale between management and ecosystem science should be considered in tradeoffs used to inform ecosystem-based management.

2.2 INTRODUCTION

A primary challenge for ecosystem management is that ecosystem services are not independent and attempting to optimize a single service may lead to reductions in other services (Holling and Meffe 1996, Rodriquez *et al*. 2006, Bennett *et al*. 2009). Traditional management aims to enhance the delivery or production of a single particular service. In doing so, interactions between ecosystem services may create tradeoffs, where the delivery of one service reduces delivery of another (e.g. harvesting trees for timber may reduce habitat for some wildlife species). Identifying and evaluating important interactions between ecosystem services are essential for exploring scenarios for achieving better ecosystem management and conservation objectives (Pikitch *et al*. 2004, Carpenter *et al*. 2009, Link 2010). As such, there has been a recent emphasis toward considering more holistic management strategies that consider multiple services and the interactions between them (Pikitch *et al*. 2004). However, in order to implement holistic management, we need to understand how ecosystem services interact and identify situations where either strong or weak tradeoffs prevail (Carpenter *et al*. 2009).

A challenge for evaluating tradeoffs is that complex ecological interactions and uncertainty in observations and ecological mechanisms render many tradeoffs difficult to observe and quantify. Some ecological interactions such as indirect effects (e.g. competition among species) or density-dependent processes can be difficult to quantify if a full range of densities are not observed or if environmental influences dominate the variability (Brook and Bradshaw 2006, Carpenter *et al.* 1994). Uncertainty in the functional form (i.e. linear, saturating, etc.) of underlying mechanisms and around stochastic processes that drive ecological relationships has the potential to fundamentally alter the shape of tradeoffs. In many studies, ecosystem structure and provisioning services are assumed to follow a linear relationship (Koch *et al.* 2009, Bennett *et al.* 2009). Linear relationships may be favored by statistical parsimony when variability is high or only a narrow range of values are observed even when the underlying process may be non-linear (Carpenter *et al.* 1994). Yet, nonlinearities are common in ecological studies and these relationships can generate strong shifts in the balance of competing objectives. Importantly, the form of these ecological relationships could fundamentally alter the optimal management solutions, and incorrect assumptions about the underlying mechanisms could lead to ineffective or inadequate management (Bennett *et al.* 2009, Farber *et al.* 2002, van Jaarsveld *et al.* 2005). Understanding the form of ecological production functions remains a limitation for improving management of multiple ecosystem services (Daily and Matson 2008).

Evaluating tradeoffs often involves reconciling differences in scale between ecosystem science and management (Nelsen *et al.* 2009). Ecosystem studies, particularly those whose purpose is to reveal mechanism, are often carried out at small spatial and temporal scales, and may lack generality. On the other hand, management of natural resources often operates at landscape or regional scales. Ecological processes operating at smaller scales may distort how management actions manifest as ecosystem benefits. Therefore, considering how the mechanisms driving ecosystem service production translate across scales is critical for managing tradeoffs among competing ecosystem services (Nelsen *et al.* 2009).

Annual returns of Pacific salmon (*Oncorhynchus spp.*) to rivers around the Pacific Rim have huge economic, subsistence, and cultural value. While annual returns of salmon are the basis of valuable commercial fisheries, salmon play several critical roles in the freshwater ecosystems to which they return (Schindler *et al.* 2003). In particular, adult salmon provide important energy subsidies to consumers such as bears, gulls, and stream dwelling resident fish (Scheuerell *et al.* 2007, Bentley *et al.* 2012). These salmon supported ecosystem services have substantial economic value in the form of hunting of coastal brown bears, wildlife viewing, and valuable sport fisheries for salmon and trout (Duffield *et al.* 2007). However, while these ecosystems are often very well managed for maximizing commercial harvest opportunities of salmon, management does not explicitly consider the potential tradeoffs between these competing values, despite increasingly active calls to do so (Darimont *et al.* 2010).

Nonlinear ecological relationships control the effects of salmon spawning on ecosystems and salmon population size. At the landscape scale, coastal brown bear populations benefit from spawning salmon (Mowat and Heard 2006) but this response may saturate at high spawning densities (Levi *et al.* 2012). In streams, resident trout rely on salmon eggs for the majority of their annual growth (Scheuerell *et al.* 2007). At low spawning densities, salmon effectively bury their eggs in the gravel, where they are not vulnerable to consumers like trout. With increasing spawning density salmon compete for available habitat and begin to dig on top of the redds (nests) of previously spawned salmon. This dislodges eggs from the gravel and leads to an exponential increase in the availability of eggs for consumers like trout (Moore *et al.* 2008). However, the ability of trout to consume and assimilate this massive flux of eggs is constrained by their digestive capacity (Bentley *et al.* 2012). This results in a complex sigmoid relationship between the growth of resident trout and salmon spawning density. Nonlinear relationships also control population size and harvest for adult salmon. Competition among adult salmon for limited spawning habitat (described above) and among juveniles for resources in their rearing lakes reduces per-capita production at high spawning densities. The number of salmon produced saturates and can even decline as the number of spawning adults increases (Ricker 1954). Therefore, while there appears to be clear benefits to trout of additional spawning salmon, the tradeoff between harvesting adult salmon and this ecosystem benefit is complex.

In this study, we evaluate the tradeoffs between harvesting sockeye salmon in commercial fisheries and the foraging opportunities for trout presented by sockeye salmon egg subsidies. This is an ideal system to explore complex issues associated with ecological tradeoffs, such as nonlinear relationships, uncertainty, and differences in scale. Additionally, this particular tradeoff has important economic consequences, as resident trout are the primary targets of valuable sport fisheries. Would a more holistic management approach focused on balancing trout growth and commercial harvest look fundamentally different from the current management system whose goal is to maximize the long-term commercial harvest of salmon? We apply a simulation modeling approach that is embedded in rich data sets from both commercial salmon fisheries and the freshwater ecosystem. We compare these two ecosystem services using a production possibilities frontier (Silberberg and Suen 2000), typically used in economics, to evaluate the potential impact of different management policies on the relative benefit for these two competing ecosystem services. We also compare outcomes if these tradeoffs were driven by linear interactions as is often assumed.

2.3 METHODS

Study system and management

Tradeoffs evaluated in this study are based on empirical datasets on sockeye salmon population productivity, management of the commercial fishery, and resident trout growth in streams from the Wood River system of southwest Alaska. The Wood River is one of nine major sockeye salmon producing rivers in the Bristol Bay region of Alaska. It supports a healthy commercial salmon fishery as well as recreational fisheries for resident rainbow trout (*Oncorhynchus mykiss*), Arctic char (*Salvelinus alpinus*), and Arctic grayling (*Thymallus arcticus*), collectively referred to as resident trout. An average of 4.7 million sockeye salmon returned from the ocean to spawn in streams, rivers, and on lake beaches of the Wood River system between 1975 and 2015. Detailed research on resident trout as well as extensive annual monitoring of individual populations of returning sockeye salmon by management makes it an ideal system in which to assess this tradeoff.

The commercial salmon fishery operating at the mouth of the river is managed with the goal of producing MSY for sockeye salmon populations. Management is based on an escapement goal strategy, where managers target a specified number of sockeye to let ‘escape’ the fishery and enter the spawning grounds. Sockeye salmon are visually counted as they enter the freshwater system from an elevated onshore tower. Area managers open and close the commercial fishery on a daily basis in order to stay on target to achieve their specified escapement goal. In practice, there is a range of acceptable escapements bracketed by upper and lower escapement bounds. Escapement goals are set by the Alaska Department of Fish and Game based on stock-recruitment relationships for the Wood River stock (ADFG 2016).

Sockeye salmon stock-recruitment and commercial fishery yield

Density-dependence in sockeye salmon population production is estimated by a Ricker stock-recruitment relationship (Ricker 1954). Returns from an individual brood, due to staggered age structure, are reconstructed using age and genetic information of both fish sampled via beach seine as they pass the counting tower and fish harvested in the commercial fishery (Cunningham *et al.* 2017*)*. Escapement goals for sockeye populations are based on a Ricker stock-recruitment relationship fit to returns and escapement. We fit a Ricker stock-recruitment relationship to the Wood River sockeye salmon stock for returns between 1975 and 2015. Sockeye returns, *R*, as a function of the spawning population (escapement), *E*, is given by

$$\mathrm{R} = \mathrm{E}e^{\alpha * \left(1 - \frac{\mathrm{E}}{\beta}\right)} \tag{1}$$

Where α is the productivity of the population and β is the capacity of the population. In this formulation, β, is equal to the unfished equilibrium stock size E_m, or the average return expected with no exploitation. From Hilborn (1985), the escapement that produces MSY, E_{msy}, can be very accurately approximated by

$$E_{msy} = \beta(0.5 - 0.07\alpha) \tag{2}$$

We fit this stock-recruitment relationship using Bayesian Markov Chain Monte Carlo (MCMC) estimation. We informed the equilibrium population size (β) using a diffuse normal prior centered around 3 million adult sockeye (Cunningham *et al*. 2015) estimated from paleolimnological sampling of historical salmon abundances (Rogers *et al*. 2013). Posterior samples for α, β, and σ were used to generate parameter values for stochastic simulations (*see Simulation Model section*). Models were fit using the software Just Another Gibbs Sampler

(JAGS v.4.3; Plummer 2017) in R (R Core Development Team 2017). We ran three chains, each for 1,000,000 iterations thinning every 100 samples. All parameters passed model convergence criteria.

Sockeye spawning density

While adult sockeye spawn in rivers, streams, and lake beaches, the primary benefits to trout comes from populations spawning in streams and rivers. Individual stream sockeye spawning densities are estimated from annual spawning ground surveys where salmon are counted at peak spawning combined with stream habitat area surveys. We include counts for 22 streams surveyed annually from 2006 to 2016. We calculated stream-specific spawning densities by dividing the sum of live and dead sockeye salmon from each annual survey by the product of the average wetted width and the total length the survey. Peak spawning counts are an index of the total run to a particular stream. But, the total run to a stream is tightly correlated with the peak live and dead count (R^2=0.95, Davis 2015). The total run to a stream is equal to 1.72 times the peak live and dead count (Davis 2015).

We calculate watershed-wide spawning density (for deterministic tradeoff curves) from the portion of escapement destined for rivers and streams and total river and stream spawning habitat. Using data from aerial surveys between 2009-2016, we estimate that about 50% of the total escapement to the Wood River system on average spawns in rivers and streams, ranging from 40% to 70% each year (unpublished data). The total spawning habitat in rivers and streams within in the Wood River watershed is 2.4 million m^2 (Burgner *et al*. 1969). We calculate a watershed-wide spawning density (assuming an even distribution) by dividing the river and stream portion of escapement (50%) by the total river and stream habitat area. We also correct for the difference between escapement and surveys by dividing by 1.72, which makes this watershed spawning density directly comparable to the density observed in the growth response.

We tested whether the distribution of spawning densities observed across all streams in our study changed as a function of escapement. We fit lognormal distributions to histograms of spawning density among our 22 study streams from each year. We fit these distributions using the package ‘mixdistr’ in R (R Core Development Team 2017). We then estimated changes in the mean and standard deviation of those annual spawning density distributions against system-wide escapement using linear regression. There was a significant relationship between the mean spawning density and log-escapement, but not between the variation in spawning density and log-escapement (Supplementary Figure 1).

Resident fish growth in streams

Most annual growth by resident trout in the Wood River system is achieved during the late summer when they binge feed on the eggs and carcasses of spawning sockeye salmon. Using the data and methodology of Bentley *et al*. (2012), we included five additional years of data and fit multiple possible relationships (linear and non-linear) between resident fish growth in streams and salmon spawning density. Here we provide a brief overview of those methods. We sampled resident trout and grayling populations in two streams, Hidden and Lynx creeks, for diet, size distributions, and growth several times throughout summer field seasons. We include data from the end of season surveys over 14 years. The dominant species sampled were rainbow trout (*Onchorhynchus mykiss*) and Arctic grayling (*Thymallus arcticus*) and all subsequent analyses were carried out by species. We estimated the relationship between resident fish instantaneous growth from all captured individuals and sockeye spawning density in Hidden and Lynx creeks.

We tested linear, saturating, and sigmoid mixed effects models and compared them using AIC model selection. Bentley *et al.* (2012) tested models including different forms of a temperature effect on growth, but they found no significant impact, therefore we did not include models with temperature here. Sigmoid and saturating functional forms were estimated using the following form:

$$\mathrm{G} = \mathrm{g}_0 + \frac{g_m * \mathrm{S}^{\mathrm{b}}}{\mathrm{S}_0^{\mathrm{b}} + \mathrm{S}^{\mathrm{b}}} \tag{3}$$

where G is trout instantaneous growth, S is the sockeye spawning density, $\mathrm{g}_0$is the growth rate at a sockeye spawning density of zero, g_m is the maximum growth rate, S_0 is the half-saturation spawning density, or in a sigmoid relation it is the breakpoint, and b determines the steepness of a sigmoid. If b is equal to one the relationship is saturating. Updated model selection tables and parameter values are included in Supplementary Tables 1 and 2.

Simulation Model - Assessing tradeoffs

To evaluate the shape of tradeoffs between commercial fishery yield and resident fish growth, we compared the surplus production for the commercial fishery against resident fish growth (increase above g_0) at different target escapement levels using a production possibilities curve framework (Silberberg and Suen 2000). For different escapement targets between 0 and E_m, the commercial yield is plotted against the salmon-supported resident fish growth. Because these values are not directly comparable we standardized the values of commercial yield and resident fish growth to their theoretical maximums; MSY in the case of commercial yield, and g_m for resident fish growth (Levi *et al.* 2012, Richerson *et al.* 2010). We first compared the tradeoffs at the watershed scale where escapement distributes evenly across all available spawning habitats.

We next used a simulation modeling approach to incorporate stochastic population processes and parameter uncertainty to investigate a more realistic tradeoff. There were two primary simulation components. One component that drives sockeye salmon population dynamics, management, harvest. and escapement. A second that distributes spawning salmon to individual streams and estimates spawning density and resident fish growth. Sockeye salmon population dynamics were driven using the observed stock-recruitment relationship equation (1). For each simulation, we randomly selected an α and β pair, from sampled MCMC posterior distributions. We incorporated lognormal recruitment stochasticity in proportion to the observed variation. Each simulation had a management escapement target, if a simulated annual sockeye return was smaller than the escapement goal, no fishery would occur and harvest would be zero. If the run was bigger than the escapement target, escapement was determined by multiplying the escapement goal by management error. In salmon management, observed escapements often exceed management targets, particularly when sockeye runs are large. We simulated management error by multiplying the escapement goal by a lognormal deviation. The mean of the lognormal management error multiplier (μ_m) was taken from a piecewise function describing the mean as a function of the recruitment deviation (d_r; Supplementary Fig. 2).

$$\mu_m = \begin{cases} 0 & d_r < 0 \\ \exp(0.1 * d_r) - 1 & d_r > 0 \end{cases} \qquad (4)$$

For below average recruitment deviations, management error followed a lognormal distribution with a mean of 1 (i.e. escapement was centered on the escapement target). With above average recruitment deviations, mean management error increased to a maximum of 1.4.

Supplementary Figure 2 shows this management error multiplier changes as a function of the recruitment deviation. Commercial fishery harvest was calculated as the total run minus the realized escapement. Realized escapement of salmon generated future salmon runs through equation (1).

We used the relationship between escapement and mean spawning density (Supplementary Figure 1 A) in conjunction with the average standard deviation of the distributions of spawning densities in streams (Supplementary Figure 1 B) to generate distributions of spawning densities in streams for stochastic tradeoff simulations. For each simulated year's escapement, we generated spawning densities for 20 theoretical streams. Resident trout growth in each stream was calculated from the sigmoid growth response in equation (3). We incorporated parameter uncertainty in the sigmoid growth response by including randomly generated normal deviations in both the growth increase and the breakpoint from the standard deviations of parameter estimates in equation (3) (Supplementary Table 2). We ran two scenarios concerning whether resident fish can or cannot move to exploit patchy high density spawning aggregations. In the no movement scenario, system-wide growth rate was the mean growth across all streams. To simulate movement, system wide growth rate was the mean growth across streams weighted by the relative spawning density achieved in each stream. This approach does not explicitly say how much movement should occur, but rather, demonstrates the qualitative effect that resident fish movement among streams (Bentley *et al*. 2014) would induce on the tradeoff.

We ran simulations for 25 different escapement targets between 700,000 salmon (the lower escapement goal) and 4.1 million (E_m). For each escapement target, we ran 1000 simulations, each lasting 50 years (with a 1000 year burn-in period). We chose this short simulation length to capture a range in potential outcomes of a management change over a reasonable time scale. In the scenarios incorporating stochasticity, it is possible for some simulations to produce higher average commercial yield than MSY. Similarly, some simulations can also produce resident fish growth above what would be expected in the absence of the fishery.

2.4 RESULTS

Ecological relationships forming the basis of the tradeoff

The Wood River sockeye salmon run exhibited density-dependent recruitment where per-capita production was initially high, but declined with increasing escapement (Figure 2.1 A). Sockeye recruitment reached its maximum at an escapement of 2.6 million sockeye, and declined with high escapement. There was considerable variation in recruitment at all levels of escapement, a characteristic common to most stock-recruitment function. The theoretical equilibrium population size in the absence of a commercial fishery was 4.1 million sockeye (E_m) where escapement and recruitment were equal. Surplus production, or the number of salmon produced above replacement that are available for harvest by commercial fisheries, was dome shaped with respect to escapement (Figure 2.1 B). Surplus production increased rapidly with higher escapement and reached a MSY of 2.6 million sockeye, when escapement is at 1.6 million sockeye (E_{msy}). Surplus production declined from MSY more rapidly with sockeye escapement below E_{msy} than above, creating an asymmetric response in commercial yield with respect to changing escapement policies. Current management for MSY of sockeye salmon targets an annual escapement between 700,000 and 1.8 million sockeye (Figure 2.1 A,B). This general shape of the stock-recruit relationship describing population dynamics is very common among fishes and nearly universal for salmonids (Foss-Grant *et al.* 2016)

Resident trout growth increased with higher sockeye spawning densities, but the shape is distinctly nonlinear (Figure 2.1 C). In all four stream-species combinations, resident trout growth increased with higher sockeye spawning density, but reached an asymptotic maximum at high densities (Figure 2.1 C, Supplementary Figure 1). In three of four stream-species combinations we modeled, this relationship followed a sigmoid shape (Supplementary Table 1). In these cases, we observed little change in resident trout growth until sockeye spawning density increased to 0.21 salmon*m^{-2} where growth increased rapidly. Growth reached a maximum that was nearly double the rate observed at low sockeye spawning densities. One of the four relationships was best described by an asymptotic shape (Figure 2.1 C). In either form, increased growth rates for trout were nonlinearly dependent on the density of spawning sockeye salmon.

These density-dependent ecological relationships form the basis of the tradeoff between sockeye salmon harvest and escapement. The relative fishery yield and relative resident trout growth as a function of escapement are plotted against one another in a production possibilities frontier (Silberberg and Suen 2001, Figure 2.1 D). The curve progresses counter-clockwise from low escapement (high commercial harvest rate) in the lower left corner to E_m (zero harvest) in the upper left corner. E_{msy} is associated with a spawning density of 0.19 salmon*m^{-2}, very close to the breakpoint in the resident fish growth function. Escapement below E_{msy} results in spawning densities less than this breakpoint resulting in no increase in resident fish growth. Resident fish growth increases with escapements up to about 2 million fish, with a less than 10% reduction in commercial yield. Escapements below E_{msy} are suboptimal (not efficient allocations), as they would both decrease commercial yield and result in slower resident fish growth than those achieved at E_{msy}. While typically not included in the curve, we included these suboptimal points because returns can be smaller than E_{msy} (thus escapement is less than E_{msy}) and this includes the lower escapement goal bound for this system. These two ecological relationships produce a very sharp tradeoff as a relatively small change in escapement can dramatically change the relative growth of resident trout.

Important controls on the shape of the tradeoff

The shape of the tradeoff between commercial yield and resident trout growth is determined by the underlying ecological functions (Figure 2.2 A). We observed two different relationships between resident trout growth and sockeye spawning density, sigmoid and saturating (Figure 2.1 C), but other studies assume a linear ecological production function. Solutions below E_{msy} using any of the three functional forms are suboptimal as they result in both lower resident trout growth and commercial fishery yield. However, at the lower escapement goal bound a saturating response results in more than double the resident trout growth than the linear form. Resident trout growth in the linear functional form increases monotonically to a maximum with no commercial fishery and at E_{msy} only 40% of the maximum growth is achieved. Due to the rapid increase in growth at low spawning densities in the saturating relationship, resident trout growth is at 75% of the maximum at E_{msy}. The linear or saturating forms result in smoother shifts in the tradeoff as escapement changes.

Both sockeye salmon population productivity and resident trout growth are dependent on the density of spawning sockeye salmon, but the difference in the spawning density that controls these relationships could change the shape of the tradeoff (Figure 2.2 B). If density-dependence in sockeye population production ($\delta_{Fishery}$) influences per capita production at a lower spawning density than what is required to achieve the benefit to resident trout growth (i.e. the density-dependence for resident fish growth, δ_{Growth}), then E_{msy} would not be enough salmon to saturate the spawning grounds and increase resident trout growth (Figure 2.2 B, orange curve). Escapements above E_{msy} would strongly increase resident trout growth, at the expense of commercial fishery yield. If $\delta_{Fishery}$ is much greater than δ_{Growth}, then both commercial fishery yield and resident trout growth would be maximized at E_{msy} (Figure 2.2 B, red curve). Based on field data, we observed very similar values for $\delta_{Fishery}$ and δ_{Growth}, 0.19 and 0.21 salmon*m^{-2}, respectively (Figure 2.2 B blue curve). Importantly, the difference between density controls on the two ecological production functions distinctly changes the shape of the tradeoff between these two ecosystem services.

Escapement and sockeye spawning density in streams

There is a large difference in spatial scale between management for escapement and the resident trout growth response observed in streams. Escapement is counted at the mouth of the Wood River, but these salmon are part of many discrete populations that return to their natal rivers, beaches, and streams to spawn. Population dynamics among natal spawning habitats are uncorrelated (Rogers *et al*. 2008). We observed escapements between 740,000 and more than 4 million (the expected escapement in the absence of a commercial fishery, E_m), between 1955-2012 (Figure 2.1 A). We evaluated how stream specific sockeye runs and spawning densities were related to increasing escapement (Figure 2.3). Increased escapement resulted in higher spawning densities, but there was considerable variation among streams. Spawning densities in streams were highly variable in both low and high escapement years, but all distributions followed a similar pattern, many streams with low spawning densities and few with higher densities (Figure 2.3). In high escapement years, more sites had intermediate spawning densities, but much of the escapement was present in very dense spawning aggregations (2.0 salmon*m^{-2} or greater). The proportion of streams that exceeded the density required to saturate the spawning habitat (0.21 salmon*m^{-2}) increased with escapement (Figure 2.3 inset). At the lower escapement bound 20% of streams reached saturating densities. In the two largest escapements, including 4 million sockeye, less than 60% of streams reached saturation. The unfished equilibrium stock size for this population of 4.1 million, would likely not saturate all streams due to asynchronous population dynamics among streams.

Including stochastic processes in the tradeoff

Incorporating stochastic ecological processes changed the shape of the tradeoff between resident trout growth and commercial yield such that altering the escapement target resulted in less severe changes in resident trout growth than what was suggested by the underlying sigmoid relationship (Figure 2.4). Additionally, there was an overall improvement in the tradeoff as resident trout growth was increased at lower levels of escapement due to some streams being oversaturated in low escapement years. The resident fish growth achieved at E_{msy}, was 75% of the maximum (Figure 2.4). At the lower escapement bound resident fish growth was 40% of the maximum as opposed to zero in the deterministic tradeoff curve. Escapements greater than E_{msy} resulted in increased resident fish growth, but steep declines in commercial yield. Increasing resident growth from 75% to 90%, reduced commercial yield by 40%. There was a wide range of escapements that produced greater than 80% of the theoretical maxima for both commercial yield and resident fish growth (Figure 2.4). Most of the sources of stochasticity, like management implementation error, and variability in sockeye production increased the variability and resulted in a wide range of achieved resident fish growth or commercial yield for most escapement targets. However, these sources did not did not alter the underlying shape of the tradeoff.

Mobile consumers can move to exploit patchy resources in their environment. The stochastic tradeoff curve presented in Figure 2.4 assumed that resident fish did not move to exploit spatial variability in the saturation of different streams. Allowing resident fish to move to exploit the saturating streams increased the growth benefit for resident fish at low escapements (Figure 2.5). The exact shape of the tradeoff curve depended on the degree of movement and competition between individual resident fish for feeding positions in streams. But, any movement of resident trout to capitalize on streams that are oversaturated with spawning salmon further softened the tradeoff between the benefits for resident trout growth by spawning salmon and harvesting salmon in commercial fisheries.

2.5 DISCUSSION

The goal of this study was explore how the nature of the interactions between competing ecosystem services influenced the tradeoffs considered in alternative management strategies. Our analysis revealed that density-dependence and differences in scale between management and ecological functions strongly influence the shape of tradeoffs and optimal management solutions. Together these processes create a much weaker tradeoff and a situation where a single-objective management system focused on producing MSY of sockeye salmon simultaneously achieves a remarkably good ecosystem outcome and harvest for commercial salmon fisheries.

Density-dependence and nonlinear tradeoffs

Density-dependence strongly influenced the shape the tradeoff and balance of these two competing ecosystem services. Salmon populations generally exhibit density-dependence and the management of the salmon fisheries generally tries to minimize density-dependence on the spawning grounds (Hilborn and Walters 1992). As densities increase, territorial females are less able to competitively exclude other salmon and new nests are superimposed on top of old nests, dislodging previously buried eggs. If superimposition is a primary control on population productivity, the management for MSY would try to minimize spawning ground over-saturation, which would occur near E_{msy}. Salmon densities at E_{msy} are very close to the important thresholds for resident trout growth as superimposition leads to the non-linear increase in the availability salmon eggs for resident fishes (Moore *et al*. 2008). In this system, E_{msy} results in a spawning density of 0.19 salmon*m^{-2} which is very close to the saturation threshold of 0.21 salmon*m^{2} observed in streams. Here, the mechanism of density-dependence on the spawning grounds results in the same number of salmon to produce MSY and to provide ecological benefits to the ecosystem.

In general, density-dependence could serve to improve tradeoffs and soften the effects of changing management solutions. Not accounting for density-dependence, i.e. assuming a linear ecological production function, can lead to very different management recommendations. For example, Bozec *et al*. (2015) evaluated ecological tradeoffs in a system where parrotfish maintain coral cover by consuming macroalgae, a coral competitor. They showed with models that fishing reduced parrotfish biomass, which reduced consumption of algae and lead to strong negative responses in coral cover. However, decreasing biomass does not necessarily linearly reduce population consumption because consumption in the absence of fishing could be constrained by density-dependence. Increases in per-capita consumption could compensate for the change in biomass and this would serve to reduce the severity of the tradeoff. Density-dependence is likely to play an important role in ecosystem service tradeoffs across many ecosystems and should be considered when evaluating alternative management solutions.

Many studies provide strong evidence of nonlinearities in ecosystems, some of which are produced by density-dependence. Yet, considerations of ecological tradeoffs between ecosystem services often assume linear ecological production functions (Bennett *et al*. 2009, Raudsepp-Hearne *et al*. 2010). Support for a linear relationship may arise due to small sample sizes or lack of strong contrast necessary to test for more complex ecological relationships. A straight line can approximate complex relationships over constrained regions. Even when ecological dynamics are nonlinear, linear relationships may be favored by statistical parsimony when variability is high (Carpenter *et al*. 1994). Nevertheless, the functional forms of the ecological production functions determine the shape the tradeoff curve and dictate where optimal management would occur. If a linear function between the salmon subsidy and resident trout growth was assumed, we would conclude that escapements that maximize commercial yield result in relatively poor resident fish growth and that increasing escapement goals would lead to much better trout growth. Instead, the nonlinear relationships observed in this ecosystem, management for maximizing commercial yield pretty good resident trout growth, and increases in escapement would result in modest increases in trout growth with more cost to commercial yield. Accounting for and exploring potential nonlinearities is critical to the effective consideration of tradeoffs between competing interests and should be included in scenario-planning exercises, particularly for systems with weak knowledge about underlying ecological processes.

Differences in scale between management and ecosystem processes

Large differences in scale between management actions and ecological processes can influence how management changes manifest in ecosystem services. Here, at the stream scale there is a complex sigmoid growth response for resident trout to changing sockeye spawning density. However, this response does not directly derive from changes in escapement alone. Escapement is made up of dozens of discrete populations of salmon. Any return is typically characterized by many small runs and few large runs. Population variability and asynchrony drives differential spawning densities in streams. It is the spawning density in each of the individual populations that leads to increased egg availability and higher growth rates for resident trout. This variability among individual salmon populations leads to oversaturation and increased resident trout growth in some streams at low escapements, but does not necessarily lead to oversaturation in all streams with high escapement. These dynamics remove the "all-or-nothing" relationship present in the sigmoid growth response, creating a softer tradeoff. Considering how management changes translate across scales to drive ecosystem services is important for evaluating tradeoffs.

Population variability and asynchrony across the landscape also provide opportunities for mobile predators to exploit patchy resources in their environment (Armstrong *et al*. 2013, Schindler *et al*. 2013). Movement by resident fish to use spatially heterogeneous salmon subsidies could enable very high resident fish growth even under lower escapement levels. In this ecosystem, many rainbow trout and Arctic grayling have been documented moving from one tributary to another over the course of less than one day (Bentley *et al*. 2015). Our results suggest that this ability to move among streams, tracking the availability of salmon resources would further soften the tradeoff between commercial harvest and resident fish growth. The exact degree to which they can track and exploit saturated habitats across the system is not known and will depend on many factors including intra- and interspecific competition for feeding locations.

In addition to higher individual growth rates, resident fish population sizes may grow due to a long-term increase in escapement. As individuals saturate their digestive capacity, excess eggs available in streams could provide resources to more subordinate individuals. Therefore higher escapement could support larger populations of resident fish. However, other ecological processes may constrain total resident fish population size. Density-dependence in spawning habitat for trout and food resources for juvenile fish (eggs are not available to young of the year fish due to gape limitation) are likely operating in trout populations as well. Further research is needed to understand how increased escapement could lead to larger populations of trout and where other density-dependent processes in resident trout populations begin to take over.

Considering optimal allocations

A difficult challenge for managing ecological tradeoffs in an ecosystem context (Link *et al.* 2010) is that components often have non-commensurate economic values (Richerson *et al.* 2010). The economic value of some ecosystem services, such as existence value, can be very difficult to quantify (Richerson *et al.* 2010). There are non-commensurate economic values between commercial salmon fisheries and resident fish growth. In Bristol Bay, both the commercial salmon harvest and sport fisheries for resident trout have substantial economic value. While harvesting salmon have direct economic benefits for commercial fisheries, spawning salmon eggs support the foundations of the valuable sport fishery (Bentley *et al.* 2012, Duffield *et al.* 2007). However, it is difficult to translate the growth response observed for resident trout to an increase in sport fishery value. From extensive survey data, sport fishers indicate that catching a large number of fish, catching trophy fishes, and having the opportunity to catch a fish, as three of their top reasons for choosing to fish in Bristol Bay (Duffield *et al.* 2007). This lends strong support to the potential for trout growth rate to influence the value of the sport fishery, but the exact relationship is nearly impossible to quantify. However, the relativized framework here allows us to make very coarse comparisons about optimal economic solutions in this tradeoff (Mangel and Downing 2016). For example, if the economic value of resident trout growth was equal to that of commercial fishery yield, the optimal economic solution would be an escapement target where the derivative of the production possibilities curve is equal to -1. If the value of resident fish growth was half of the commercial fishery yield, the optimal solution would be where the derivative is equal to -2. In our stochastic production possibilities curve, if resident fish growth translated into a value of 20%, 50%, or 100% the value of commercial yield would result in escapement goals of approximately 1.67 million, 1.78 million, and 1.89 million, respectively. This relativized framework can be used to explore how management targets might shift under different economic valuations.

*Conclusion*s

As we continue to recognize the importance of managing ecosystems for multiple components, services, and stakeholders, we need to better understand the conditions that drive tradeoffs among these components. We need to identify ecological processes where tradeoffs are likely to be strong and those where they may be weak. Nonlinear dynamics including density-dependence have a strong influence on the shape of tradeoffs and optimal management solutions and should be explored as scenarios when assessing the consequences of different management and conservation actions.

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2.7 FIGURES

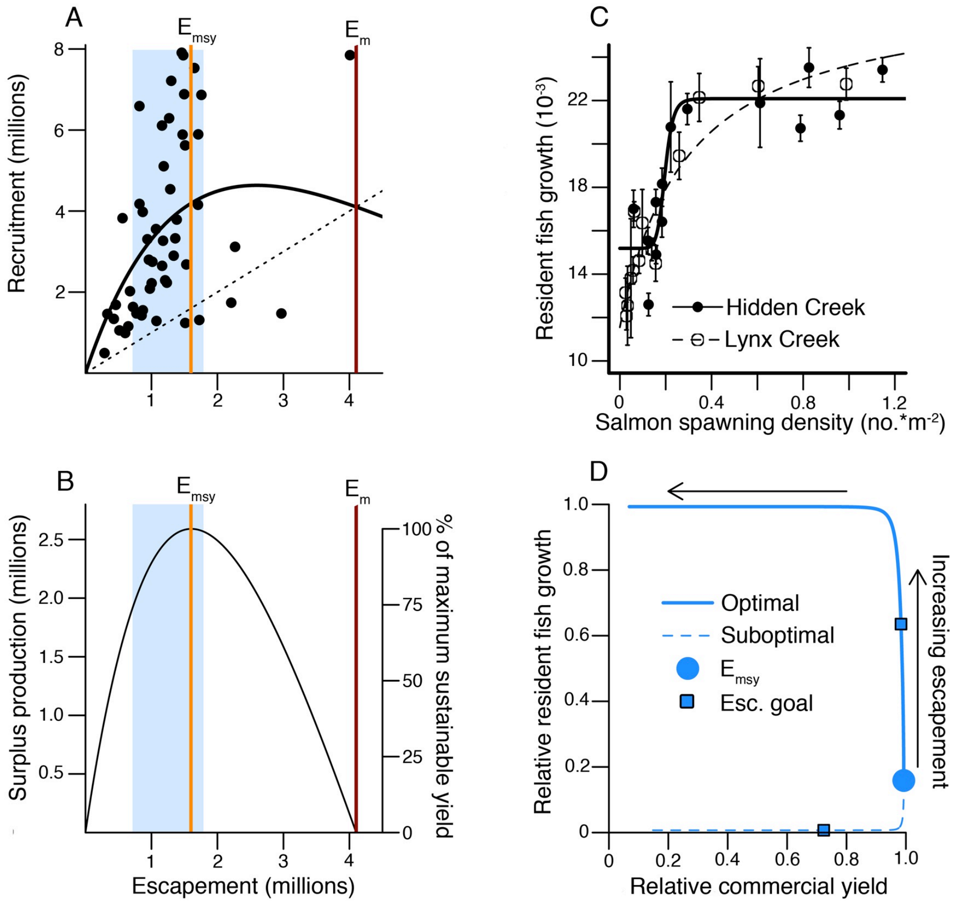

Figure 2.1: Ecological relationships forming the basis for a tradeoff between commercial salmon fisheries and trout growth in spawning watersheds. (A) Escapement-recruitment relationship for the Wood River system, Bristol Bay, Alaska. The dashed line indicates the 1:1 replacement line. The blue polygon is the escapement target range currently used in for management of the commercial fishery in this system. The orange line is the escapement that would produce maximum sustainable yield in the commercial fishery (E_{msy}) and the red line indicates the escapement that would occur in the absence of a commercial fishery (E_m). (B) Surplus production for the commercial fishery as a function of escapement based on the above escapement-recruitment curve. (C) Growth response of rainbow trout as function of spawning

density in two streams. Growth responses for Arctic grayling are in Supplementary Figure 1. (D) Production possibilities frontier for the tradeoffs between commercial fisheries and trout growth. Curve follows counterclockwise from low escapement policies to closure of commercial harvest and maximum escapement in the upper left corner. Trout growth functional form is based on a sigmoid curve. Escapement is assumed to evenly distribute across spawning habitat. Positions of the lower, upper, and Emsy escapement goals are indicated by points. Escapement targets that produce suboptimal outcomes are indicated with a dashed line (i.e. increasing escapement would improve both resident fish growth and fishery yield).

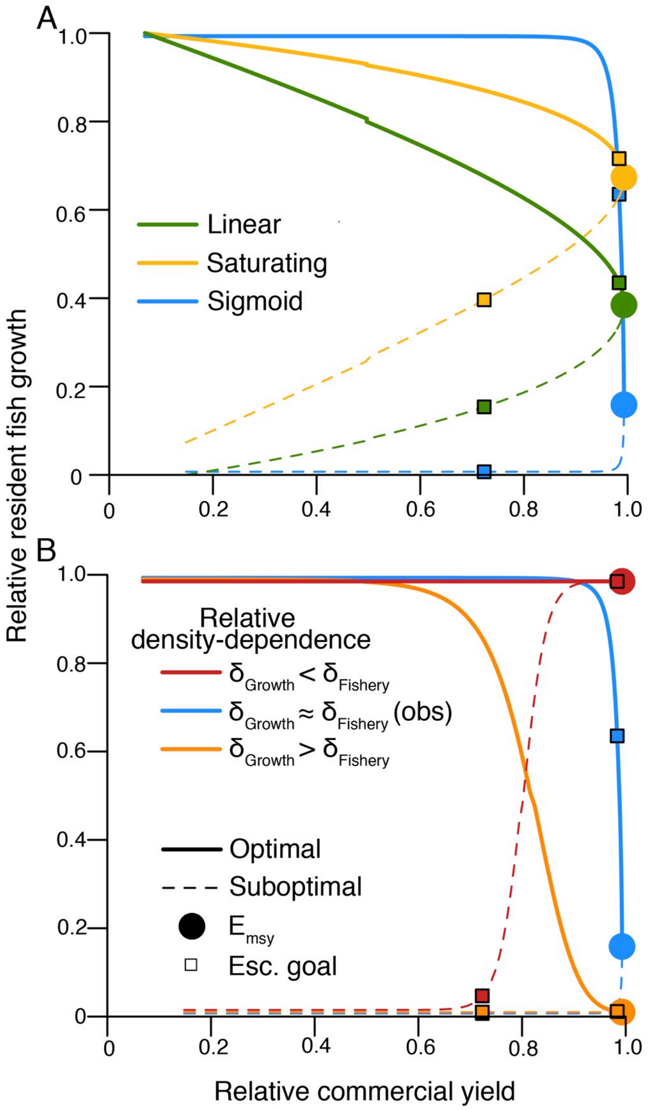

Figure 2.2: Important controls on the shape of production possibilities frontiers for tradeoffs between commercial fishery production and resident fish growth. (A) Production possibilities frontiers assuming different function forms for the resident fish growth ecological production function. (B) Production possibilities frontiers where density-dependence in the watershed (δ_{Growth}) is less than, about equal to, or greater than density-dependence in the sockeye population (δ_{Fishery}). All curves follow counterclockwise from low escapement targets to closure of commercial harvest and maximum escapement in the upper left corner. Lower and upper

escapement targets as well as E_{msy} reference points are indicated by points for each curve. Escapement targets that produce suboptimal outcomes are indicated with a dashed line (i.e. increasing escapement would improve both resident fish growth and fishery yield).

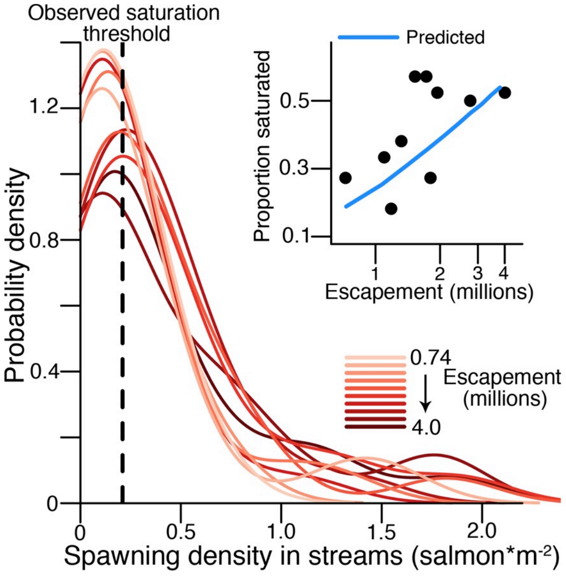

Figure 2.3: Observed spawning densities in streams from the Wood River system across a range of total escapement to the system. Fitted probability densities to distributions of spawning density in more than 20 streams for each year are color coded by total system escapement. Densities are calculated from observed counts of salmon and total spawning habitat area from stream surveys. (Inset) The observed proportion of streams reaching the saturation density as a function of escapement. Blue line indicates the predicted proportion of streams reaching the saturation density based on fitted lognormal distributions see *methods*.

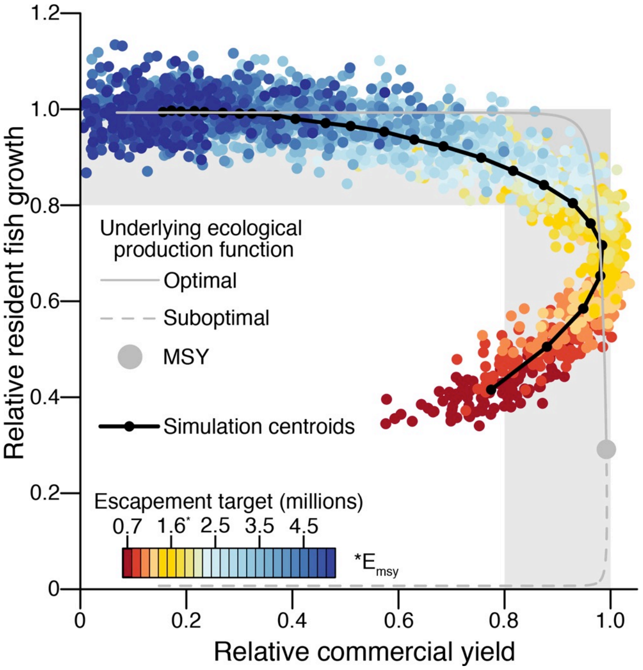

Figure 2.4: Stochastic production possibilities frontier for tradeoffs between commercial salmon fisheries and resident fish growth. Escapement targets used in each simulation are color-coded. Population dynamics are simulated using the Wood River sockeye stock-recruitment relationship (Figure 2.1 A). Total system escapement is distributed among 20 streams using simulated saturation values (Figure 2.3 inset). Resident fish are assumed to receive growth improvements in proportion to the number of streams that saturate. The sigmoid ecological benefit relationship is used for resident fish growth in streams according to simulated saturation values. Grey boxes indicate regions above 80% for each of the two axes.

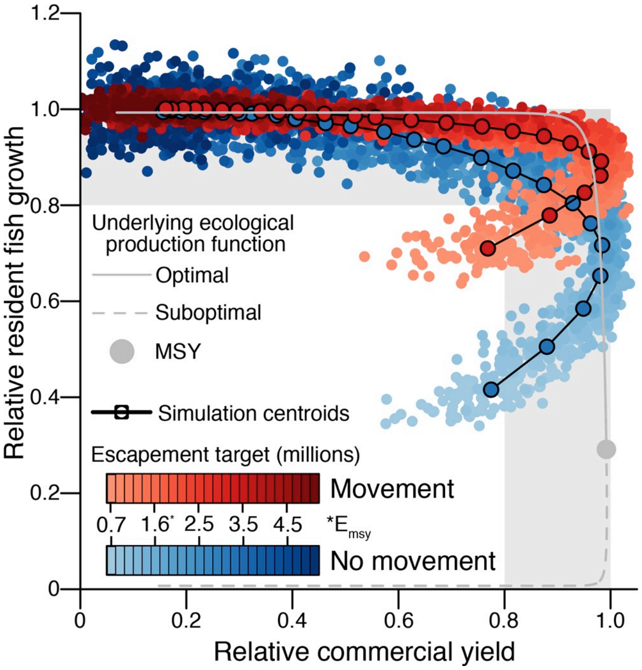

Figure 2.5: Stochastic production possibilities frontiers under two scenarios of resident fish movement. Total system escapement is distributed among 20 streams using simulated saturation values (Figure 2.3 inset). With no movement (blue), resident fish stay in their streams and receive growth improvement in proportion to the number of streams that saturate. With movement (red), resident fish move to exploit patchy resources and receive benefits in proportion to the weighted average of stream saturation values. This represents one possible realization of fish movement, but all levels of movement with change the production possibilities curve from blue towards red. The sigmoid ecological benefit relationship is used for resident fish growth in streams according to simulated stream saturation values. Grey boxes indicate regions above 80% for each of the two axes.

Chapter 3. Watershed geomorphology affects density-dependent habitat selection of spawning sockeye salmon

3.1 ABSTRACT

Habitat selection in animals controls many important ecological processes. Individuals distribute themselves among habitats that vary in resources, risk, and competition in order to complete their life cycles. The relative balance of these drivers has consequences for ecological processes such as growth, predator-prey interactions, fitness, and population productivity. Empirical studies of the degree to which habitat use is controlled by conspecific interactions are rare due to the scale and intensity of data collection needed to quantify individual responses to abundance. A further challenge is to quantify how habitat features influence density-dependent habitat patch selection in real ecosystems. In this study, we evaluate how the spatial distribution of spawning sockeye salmon (*Oncorhynchus nerka*) changes as their population abundance varies over an order of magnitude. We also ask to what degree this relationship is controlled by intrinsic differences among habitats as controlled by watershed geomorphology. Using high-resolution annual surveys of 18 distinct populations of sockeye salmon that spawn in streams that vary across a range of geomorphic conditions, we found that habitat use was patchy under low abundance conditions and became increasingly even as abundance increased, much like a *basin model* of habitat selection would predict. This effect was strongest in high gradient streams, where there are presumably larger differences in the intrinsic quality among alternative habitat patches. This result has consequences for population productivity in streams, the availability of salmon subsidies for ecosystems, and for establishing goals for habitat restoration.

3.2 INTRODUCTION

Habitat selection by individual animals controls many ecological processes and critically affects population dynamics (Pulliam and Danielson 1991, McPeek *et al.* 2001). Individuals actively select among habitats that vary in opportunity, risk, and competition to complete their life-cycles (Fretwell and Lucas 1970, Morris 1989). Individuals compete and interfere with each other for high quality habitat patches, thus the optimal strategy for using habitat must depend on the strategy of other individuals, and the quality of individual patches of habitat, and on population abundance. The spatial distribution of animals that results from variation in habitat patch quality, and competition among individuals for high quality feeding or breeding habitat patches has consequences for population dynamics and ecosystem functions (Rodenhouse *et al.* 1997). For example, habitat selection among foraging areas controls feeding and growth rates, and predator-prey interactions (Rozenzweig 1991). Habitat selection also occurs for high quality spawning habitats and influences individual reproductive success and population productivity (Danchin *et al.* 1998). For species that aggregate during reproduction, and are vulnerable to predation during this time, how individuals distribute across habitat can have profound effects on predator foraging success. Understanding the relative influence of habitat quality and density-dependent processes is a major challenge towards understanding how populations use habitat as their abundances fluctuate, and is important for conservation and management.

The theory of density-dependent habitat selection assumes that animals will select among available habitat patches in order to maximize their individual fitness (Morris 1989). The dominant theoretical framework for density-dependent habitat selection and resulting spatial distribution is the ideal free distribution (IFD; Fretwell and Lucas 1970). It assumes that animals can observe all available habitat patches and identify the best one, they can move between habitat patches with no cost, and that all individuals are equal competitors. The IFD distribution implies equal fitness among individuals, as any difference would be offset by movement to a more profitable patch. All of these assumptions may not be valid in all organisms and ecosystems and several variations on the IFD have been proposed to deal with violations of these assumptions (Fretwell and Lucas 1970, Tregenza 1995). Nonetheless, the IFD can describe a wide variety of observed animal distributions (Shepherd and Litvak 2004).

The spatial distribution resulting from individual habitat selection depends on the relative quality of different habitat patches (Morris 1987). Habitat suitability is the result of a complex interaction between intrinsic habitat patch potential and variable responses of habitat patch quality to abundance; increasing density in any habitat patch will reduce its suitability (Fretwell and Lucas 1970). Habitat selection by individuals balances intraspecific competition with intrinsic potential among habitat patches, resulting in different spatial distributions. Two common models for describing how habitat patches vary in their intrinsic potential and response to density are: habitat patches have the same intrinsic potential (r), but different carrying capacities (K) (constant r and variable K); and habitat patches differ in their intrinsic potential and their carrying capacities (variable r and variable K, Figure 3.1 A,B). Each of these models results in specific predictions for habitat use and spatial distribution of animals with increasing population size. With constant r and variable K, all available habitat patches become occupied at low population abundance because they are similar in intrinsic potential and conspecific interference is negligible. As population size increases, the spatial distribution remains the same as each patch receives individuals in proportion to the resources available in that patch (Figure 3.1 C). This is known as the *proportional-density model* (Shepherd and Litvak 2004). With variable r and variable K, the patches with better intrinsic potential are occupied preferentially until their suitability declines due to competition such that individuals spill over to occupy patches with lower intrinsic potential (Figure 3.1 B). The resulting spatial extent increases with population size and habitat use becomes more even across the landscape of habitat patches (Figure 3.1 D). This is referred to as the *basin-model*; as population size decreases occupied patches contract to a core basin (Petitgas 1998). These different patterns of patch suitability (i.e., as described by the proportional density model versus the basin model) affect the spatial distribution of animals, which has consequences for population productivity, conservation, and management of ecosystems.

Throughout their range, sockeye salmon (*Oncorhynchus nerka*) support valuable commercial and subsistence fisheries and are ecologically important for coastal freshwater ecosystems. As adults, they spend the majority of their life in the ocean, but return to their natal freshwater habitats to spawn. Spawning salmon provide an important energy subsidy for the ecosystems they return to (Schindler *et al.* 2003). In parts of their range, salmon populations have declined due to habitat loss and alteration. Substantial effort has been put into restoring spawning habitats to improve population sizes (Katz *et al.* 2005). However, habitat use may depend on both the quality of all available habitats (natural and restored) and population size. Understanding the spatial ecology of spawning sockeye salmon and the influence of density-dependent habitat selection is important for understanding the effectiveness of expensive restoration efforts in improving endangered populations.

In this study, we evaluated how sockeye salmon populations distribute among available spawning habitats as their populations vary by more than an order of magnitude between years. We used annual peak spawning counts from 18 discrete sockeye salmon populations in the Wood

River system in the Bristol Bay region of Alaska. Populations included in this study fluctuate in size by more than an order of magnitude between years. Each salmon population spawns in their natal streams, which encompass diverse spawning habitats ranging from low gradient warm streams to high gradient cool streams (Pess *et al.* 2016). Each of these habitats may offer different intrinsic potential fitness and impose different constraints on populations. Spatial variation in intrinsic potential among habitat patches should be controlled by stream gradient (Montgomery *et al.* 2011, Burnett *et al.* 2007). We test whether the relative distribution of intrinsic potential among patches and the response of each population's spatial distribution to increasing population size is controlled by this geomorphic gradient. We use an evenness metric to measure changes in spatial distribution and habitat usage at different population abundances (Payne *et al.* 2005). Relative suitability among habitat patches and the resulting spatial distributions should manifest as changes in spatial evenness as population sizes increase (Figure 3.1 E,F). If habitats have the same r, as in the proportion-density model, evenness will be high at very low population abundance, but will decline and flatten at larger population sizes (Figure 3.1 E). The level of evenness at large population sizes will be determined by the differences in K among habitats. If habitats differ in their r, as in the basin-model, evenness will be low at small population sizes as individuals will occupy sites with the highest r. As population abundance increases, densities in the highest r sites will reduce habitat suitability such that it will be more profitable for individuals to move to a site with a lower r, thus evenness will increase and saturate at large population sizes (Figure 3.1 F). If differences in r among habitats are small, evenness increase rapidly at small population sizes. If differences in r among are large, evenness will increase slowly at small population sizes (Figure 3.1 F). Therefore, using changes in evenness across large differences in population size, we evaluate support for either the proportional-density model or the basin-model, and for relative differences in r among habitats.

3.3 METHODS

Study Site

We evaluated the spawning distributions of stream populations of sockeye salmon in the Wood River basin (59º20’N, 158º40’W) in the Bristol Bay region of southwest Alaska. The Wood River system is comprised of five large interconnected lakes fed by many tributaries, and eventually flows into Bristol Bay near Dillingham, Alaska. The landscape of this region is diverse with steep mountains on the north and west sides of the basin, and flat peat lands to the east and south (Lisi *et al.* 2013). Annually, in late July through early September, sockeye salmon spawn in streams, rivers and on lake beaches. A commercial fishery for sockeye salmon operates at the mouth of Wood River and harvests about half of the returning sockeye salmon, varying among years in response to the overall population size. Streams draining this diverse landscape support dozens of distinct populations of sockeye that vary asynchronously through time (Rogers *et al.* 2008), and at the individual population scale, salmon runs exhibit large interannual fluctuations in abundance (Schindler *et al.* 2010), which creates intense competition for available spawning habitat during years with strong returns.

Data collection

We conducted annual stream surveys on foot of sockeye populations during peak spawning from 2008-2017. Streams are surveyed from mouth to headwaters in 200-meter segments using a GPS unit. Live and dead sockeye are visually enumerated by 2-3 people and recorded for each segment. Most streams are less than 5 meters across, so visual detection and counts of adult salmon in these small streams are likely accurate. Each year, surveys are conducted as close as possible to a stream-specific peak spawning date (Lisi *et al*. 2013). Some years were removed from the data set because the surveys were cut short due to dangerous wildlife encounters, or in recent years, new habitats were made available by the loss of a beaver dam.

We include 18 streams in this analysis that have the longest and most complete records. These 18 streams drain watersheds that vary considerably in their average gradient. Watershed gradient controls gravel sizes and hyporheic flow, which are important components of quality sockeye spawning habitat (Quinn 2005). Watershed slope (º), which covaries with many other watershed geomorphic attributes important to salmon (Lisi *et al.* 2013) was calculated using a digital elevation model for the Wood River basin using ArcGis (v10.0, Environmental Systems Research Institute, Redlands, CA, USA). Streams varied in length from 1.4 km to 6.4 km.

Data analysis

We quantified the spatial distribution of sockeye in each year and stream using an evenness metric (Payne *et al.* 2005). We used *Lloyd's mean index of crowing* (Lloyd 1967):

$$J = \frac{V}{N^2} - \frac{1}{N} \tag{1}$$

where V is the variance in individuals across all sites, N is the mean number of individuals occupying all sites. The index is standardized between zero (perfect unevenness) and one (perfect evenness) by transforming J with:

$$\frac{1}{1+J} \tag{2}$$

This index is used to assess the average degree of crowding experienced per individual (Lloyd 1967). This metric is not sensitive to the total number of sections in a stream or total population size (above about 100 individuals which is well below any of the included counts, Payne *et al*. 2005).

To test for changes in spatial distribution with increasing population size we fit a Bayesian hierarchical model to measures of evenness (*J*) across streams (*i*) and population sizes.

$$J_{i,y} \sim N(\mu_{i,y}, \sigma_{obs}) \tag{3}$$

$$\mu_{i,y} = \alpha_i + \beta_i * n_{i,y} + \alpha_{slp} * WS_i \tag{4}$$

$$\alpha_i \sim N(\mu_\alpha, \sigma_\alpha) \tag{5}$$

$$\beta_i \sim N(\alpha_{slp} + \beta_{slp} * WS_i\, , \sigma_{slp}) \tag{6}$$

This model includes stream-specific random intercepts (α_i) and stream-specific random slopes (β_i) with respect to population size ($n_{i,y}$). To test for the effect of watershed slope (i.e., an aggregate index of geomorphic conditions) on the effect of density, the mean β_i is a function of watershed slope (WS_i). To standardize comparisons among streams of varying size, total runs to any stream were divided by the total available spawning habitat (the product of stream length and the average width). Evenness is constrained between zero and one therefore we evaluated models with both evenness and logit-transformed evenness. The importance of the different relationships we tested were the same between models, mostly due to the fact that we have few observations of evenness near zero or one. However, the interpretation is simpler with untransformed evenness, therefore we present results from only the model using untransformed evenness. Parameters for this model were estimated using Markov chain Monte Carlo methods in JAGS in R (Plummer 2017). All parameters were given very wide uniform prior distributions. We ran three chains each for 1,000,000 iterations, including 100,000 burn-in periods. All chains mixed well and all Gelman-Rubin statistics were very close to 1. We assessed the strength of relationships between evenness and density and the effect of watershed slope by evaluating parameter posterior distributions. All posteriors were well constrained and were not near the bounds imposed by their uniform priors.

3.4 RESULTS

Spatial patterns of habitat usage varied among streams (Figure 3.2). In low gradient streams, spawning salmon occupied most segments regardless of population size (e.g. Pike and Teal, Figure 3.2). In these streams, sites near the mouth tended to have lower spawning abundances than sites in the middle or upper portions of the stream. In high gradient streams (e.g. Sam, Allah, and Berm), most salmon were observed in the first kilometer, with counts generally being highest near the mouth (Figure 3.2). Habitat usage declined rapidly further upstream. In all streams, the relative spatial distributions shifted with increasing population size.

In all streams, we observed more than an order of magnitude difference in run sizes among years (Figure 3.2, red vs. blue). Large runs were typically between 10 and 40 times larger than small runs with one instance of more than 300 times. Usage of sites that were unoccupied or sparsely occupied in small run years increased with large population sizes (Figure 3.2). Despite an increase in the spatial extent of habitat use in large run years, counts in sites occupied in both small and large years increased substantially. Observed spawning densities in these sections under low run sizes were about 0.5 salmon*m^{-2}, but were in excess of 4 salmon*m^{-2} in large run years.

The distribution of habitat use, as measured by evenness across sites, increased in all streams with larger population sizes (Figure 3.3). There was no support for a negative relationship between evenness and population size in any stream. However, there was variation among streams in both the evenness under low population sizes and in the strength of the effect of population size among streams. Streams draining high gradient watersheds had lower overall evenness and a stronger response to increasing population size than streams in low gradient watersheds (Figure 3.3). This effect of population size on habitat use was saturating (log-linear relationship) indicating that changes in habitat usage was most sensitive to changes in abundance at small population sizes and effects on the spatial distribution of individuals was weaker at high abundances (Figure 3.3). This log-linear relationship supports predictions of saturating evenness of the basin-model.

Watershed slope controlled the strength of the effect of population size on the spatial distribution of spawning salmon (Figure 3.4). The median effect of watershed slope on the relationship between spatial evenness and log-population size was 0.015 and 96% of all posterior samples were greater than zero (Figure 3.4 A). Evenness increased with population size in all streams, but the effect of population size was stronger in high gradient streams (Figure 3.4 B). Due to this difference in the effect of density on spatial distribution, there was not strong support for a difference in evenness at high population densities, greater than 1 salmon*m^{-2} (the intercept of the log-linear model; Figure 3.4 C). However, streams differed considerably in their evenness at low population sizes and this was driven by watershed slope (Figure 3.4 D). Low gradient streams had a more even spatial distribution of habitat use under low populations sizes than high gradient stream where fish tended to aggregate in an increasingly smaller proportion of the habitat.

3.5 DISCUSSION

The goal of this study was to evaluate the influence of abundance on the spatial distribution and habitat use of spawning sockeye salmon and to test whether habitat characteristics controlled by stream gradient controlled the strength of this relationship. We found that, in all streams, increasing competition for spawning sites under high abundances resulted in a more even distribution of habitat use. This result is consistent with the *basin-model* where salmon occupy a core habitat during low population years, but use a larger area when spawning abundance increases (Figure 3.1, Shepard and Litvak 2004). We found no evidence for the proportional-density model and equal intrinsic potential among patches, as all relationships between evenness and spawning density were positive (Figure 3.3). We found that stream geomorphology controlled both the evenness of habitat usage with small and large populations. At low population abundances, flat streams had a more even spatial distribution than steep streams. As population size increased, density had a stronger effect in steep streams where there are apparently larger differences in intrinsic habitat qualities across the range of potential spawning habitat.

Stream gradient controls many important characteristics of quality spawning habitat for salmon such as gravel size and flow of well-oxygenated waters through the substrate (Montgomery *et al.* 1999, Bennett *et al.* 2016). Steep streams are high energy systems characterized by larger substrate and may be prone to scour following precipitation events. Some reaches in steep streams may also be prone to drying during the winter or during dry periods because larger gravel sizes enable more complete draining of the stream bed. Steep streams are more variable in their gradient, which likely corresponds to more variability in intrinsic habitat quality. In the populations studied here, at low abundances sockeye salmon were much more evenly distributed among available habitats in flat streams than in steep stream. This supports the idea that intrinsic habitat quality was more similar in low gradient streams and salmon readily occupy new habitats to avoid competition for spawning sites. In steep streams, we observed highly uneven spatial distributions at low densities, indicating more variation in intrinsic habitat quality. Dense spawning aggregations of more than 1 salmon*m^{-2} were observed in some sections even at low population sizes. There was a strong effect of density on the overall evenness of habitat use in steep streams. At high population abundance, increased density in high-quality spawning sites depressed habitat suitability such that individuals moved to suboptimal sites presumably to improve their fitness. Importantly, stream geomorphology controlled this propensity to form high density spawning aggregations. This has consequences for population productivity and availability of salmon subsidies to ecosystems.

Spawning in high densities can have negative consequences for the fitness of individuals and for population productivity. In salmon, high spawning densities leads to competition for space and superimposition of redds (nests) where females will dislodge eggs deposited by other salmon. Superimposition reduces per-capita fitness and leads to density-dependence in population productivity (Ricker 1954). In several of the streams included in this study, redd superimposition has been shown to occur at population total densities around 0.2-0.4 salmon*m^{-2} (Moore *et al.* 2008, Bentley *et al.* 2012). Density-dependent habitat selection should control the occurrence of superimposition in streams with varying intrinsic potential among habitats. In low gradient streams, due to dispersal among habitats, spawning densities should generally remain low, and superimposition would be less frequently observed under small and moderate population sizes. In steep streams, individual sections would reach high densities and superimposition should occur even under low population sizes.

Redd superimposition has important consequences for the ecology in spawning streams as it controls the availability of salmon eggs to stream consumers (Moore *et al.* 2008), an important energy subsidy for coastal watersheds. Salmon eggs may be available for stream consumers at lower population sizes in steep streams than in flat streams. Importantly, if individuals are behaving ideally, avoiding superimposition in these systems would not necessarily improve individual fitness due to the large differences in intrinsic potential among habitats. Additionally, salmon may balance fitness consequences of high-density spawning effects with fitness consequences of spawning later in the year by distributing spawning through time (Davis 2015). Changes in the evenness of habitat use as sockeye salmon populations increase will also affect the availability of salmon resources for consumers across the landscape. Stream fishes and consumers like bears can be strongly antagonistic and avoid conspecific interactions, and therefore may be limited by the spatial distribution of resources across the landscape, both among streams (Schindler *et al.* 2015) and within streams as documented here. Increases in the spatial distribution of salmon resources as salmon spread out during high abundance years (across space) may allow access for more consumers. This may enable more predators to gain access to the resource. Under the proportional-density model, territorial predators would have more access to resources, as salmon would be spread across the landscape even at low population abundances. Ultimately, stream gradient and differences in intrinsic potential among habitats controls the degree of superimposition and availability of salmon for predators and therefore salmon subsidies to freshwater ecosystems.

Density-dependent habitat selection also has consequences for habitat restoration. Billions of dollars have been spent on restoring habitat in aquatic ecosystems in the United States (Bernhardt *et al.* 2005), but the efficacy of restoration is not only dependent on the improvements in habitat characteristics. Habitat restoration initiatives usually assume that populations will readily colonize newly accessible habitat (Tentelier and Piou 2011). However, restored habitats are part of a suite of available habitats, where the relative benefits are weighed in density-dependent habitat selection. Depending on the relative quality, animals may only use restored habitats under high population densities. For Pacific salmon populations listed under the US Endangered Species Act, thousands of habitat restoration projects have been completed to improve spawning and rearing habitat in freshwater (Katz *et al.* 2005). Yet, population abundances remain low, and therefore restored habitats may remain unoccupied due to constraints in other components of their life-cycle, thereby making assessment of the success of restoration impossible. Therefore, habitat restoration may reach a point of diminishing returns if populations are not large enough to being to saturate differences in intrinsic potential among habitats and resulting in salmon to using restored habitats.

Habitat selection by individuals is the result of complex balancing of habitat quality and conspecific interference. There is considerable confusion over the predictions of the IFD for the spatial distribution of individuals among habitats that vary in quality (Shepherd and Litvak 2004). While often incorrectly referred to as density-independent, the IFD is the result of density-dependent habitat selection (Fretwell and Lucas 1970). The IFD is governed by a set of rules about how individuals assess and select habitats in order to improve their fitness. These rules play out on a landscape of habitat patches that may vary in their intrinsic potential and carrying capacity, thus the spatial distribution of animals will depend on the differences in quality among habitat patches (Figure 3.1). The IFD was originally developed to describe how foraging animals would select habitat patches (Fretwell and Lucas 1970). In spawning salmon, the quality of spawning sites is likely different due to variation in gravel size and flow. Therefore, individuals will occupy the best sites under low population sizes and spill over into lower quality sites with high population abundances, as predicted by the *basin model*. This result is predicted by the IFD when habitats differ in their intrinsic quality and carrying capacities (Figure 3.1, Shepherd and Litvak 2004).

Some of the assumptions of density-dependent habitat selection and the IFD may not be valid for all species or environments. In particular, IFD assumes that individuals are all equally competitive and therefore fitness is equal among individuals and habitats. Sockeye salmon actively defend spawning sites and coupled with variation in the size among individuals due to different life-history strategies (returning from the ocean after 1, 2, or 3 years) could lead to competitively dominant individuals. An alternative to the IFD, the ideal despotic (dominance) distribution (IDD) assumes that individuals are constrained by dominant individuals, and perceive habitat suitability accordingly (Fretwell and Lucas 1970). IDD results in unequal fitness among individuals and habitats, which influences the realized spatial distribution of animals. Two recent studies of density-dependent habitat selection in Chinook salmon (*Oncorhynchus tshawytcha*) have tested for despotic distributions with only one finding statistical support for it (Falcy 2015, Huntsman *et al.* 2017). While despotism is likely influencing fitness in sockeye salmon, the degree to which it alters habitat selection depends on the relative costs between competition with dominant individuals as opposed to occupying low quality habitats. If despotism is strong, high quality sites would likely saturate with dominant individuals and low quality sites would increase in density. Changes in the spatial distribution are likely to appear similar to large differences in intrinsic potential, and therefore identifying territorial effects on habitat selection in wild populations remains difficult. Yet, the geomorphic effect we describe here suggests that basic spatial models of habitat conditions using the IFD will allow landscape scale extrapolations of habitat use based on simple geomorphic constraints under changing population densities.

The ability to observe and detect the exact mechanisms involved in density-dependent habitat selection also depends on the spatial scale of study (Shepherd and Litvak 2004). Selection of high-quality breeding sites for salmon is likely occurring across a large range of spatial scales, down to fine-scale conditions expressed at the resolution of one to three meters. Interference among individuals at these fine spatial scales may only be important when population abundance gets high enough to saturate available habitat patches. Therefore, some stream sections with high intrinsic potential may have steep declines in suitability in response to density as the limited number of breeding patches become occupied. This could manifest in a similar pattern to that expected with uneven competitive ability among individuals. Nonetheless, our analysis shows clear effects of density on the spatial distribution of spawning sockeye salmon.

Density-dependent habitat selection in sockeye salmon has important implications for population productivity, effectiveness of habitat restoration, and ecological functions for coastal freshwater ecosystems. Here we show that increasing population size resulted in a broader spatial distribution and more even habitat use. However, the degree to which density influences the spatial distribution of spawning salmon and the propensity to spawn in high-density aggregations was related to the relative distribution of intrinsic habitat quality as controlled by stream geomorphology. Understanding how habitat quality interacts with population abundance to influence habitat use can allow managers to better predict the effects of different management strategies across diverse habitats.

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3.7 FIGURES

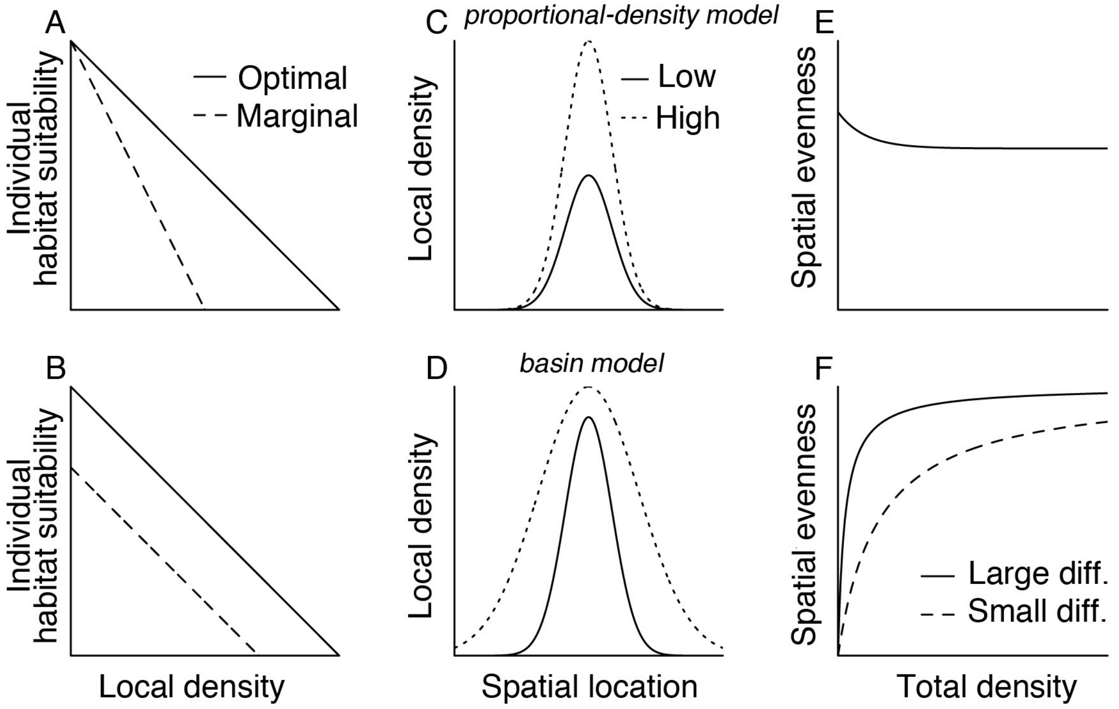

Figure 3.1: Conceptual model for two possible realizations of the IFD, the resulting spatial distributions, and effects on spatial evenness. (A) IFD where habitats have the same intrinsic potential (suitability at zero density) but different carrying capacities. (B) IFD where in both intrinsic potential and carrying capacity are different. (C) Resulting spatial distribution from panel A under low and high population abundances, commonly referred to as the *proportional-density model*. (D) Resulting spatial distribution from panel B, commonly referred to as the *basin model*. (E) The effect of population abudance on spatial evenness under the proportional density model. (F) The effect of population abundance on spatial evenness under the basin model for two hypothetical landscapes where there are either large or small differences in the intrinsic potential among habitats.

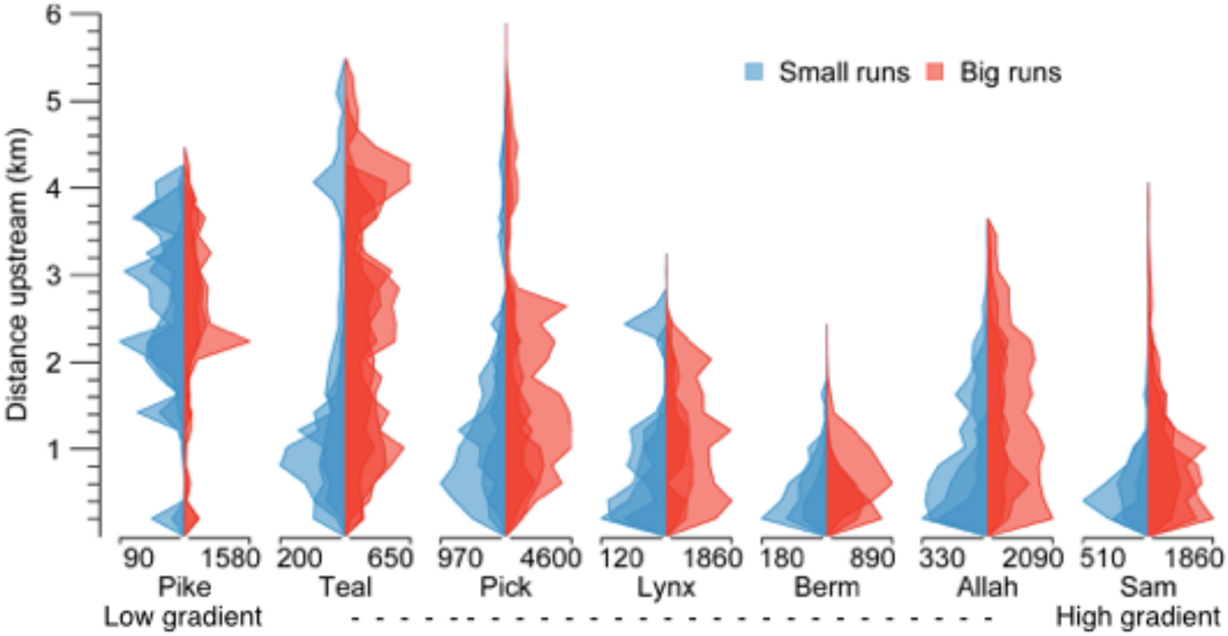

Figure 3.2: Spatial distribution of spawning sockeye salmon under different population sizes in seven streams spanning a gradient of watershed slopes. The three smallest runs for each stream are displayed in blue and the three largest are displayed in red. Streams are counted in 200-meter segments from mouth to headwaters. Streams are sorted by watershed slope from flat watersheds on the left to steep watersheds on the right.

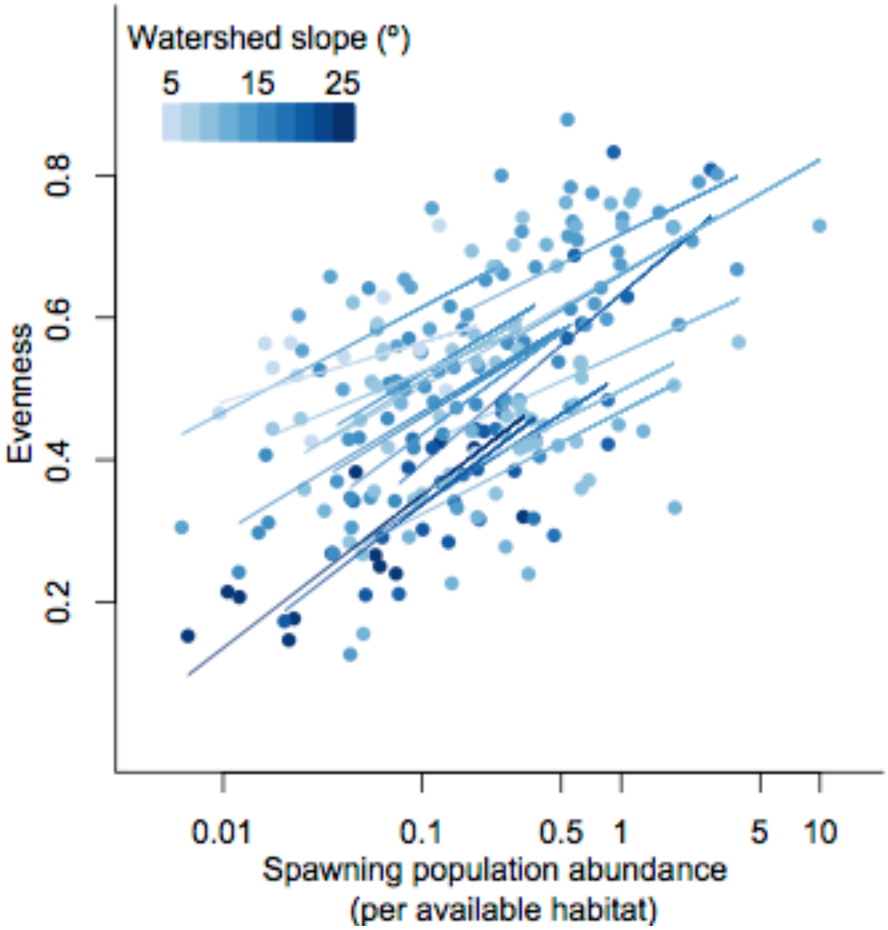

Figure 3.3: Evenness in the spatial distribution as a function of population abundance across 18 streams. Population abundance is standardized among streams to the total available spawning habitat in each stream. Watershed slopes and stream-specific regression lines are designated by color.

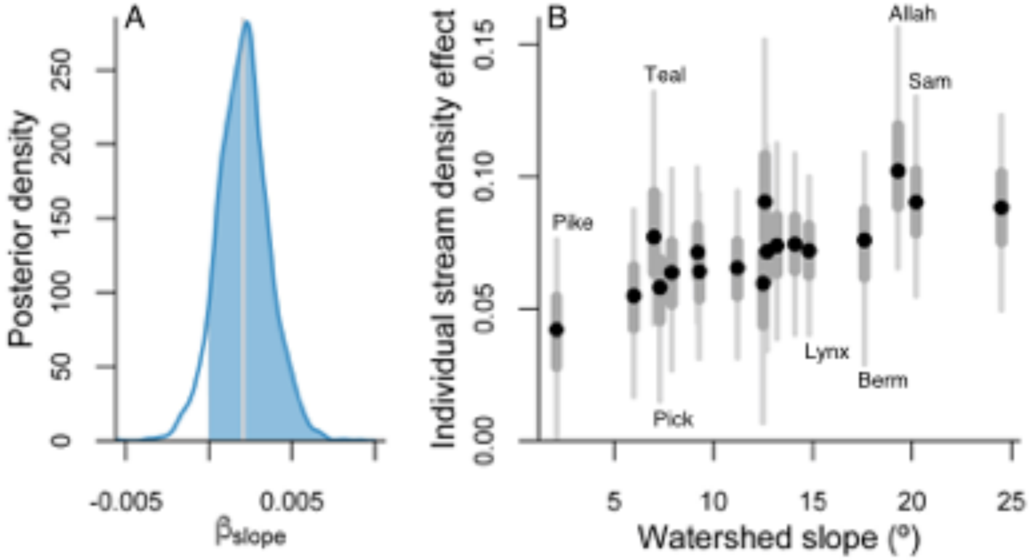

Figure 3.4: Watershed slope controls the influence of density on the distribution of salmon. (A) Posterior density for the effect of watershed slope on the density effect. The blue polygon indicates the area of the posterior greater than zero (96% of distribution). The vertical gray line is the median value of 0.002. (B) Individual stream density effects as a function of their respective watershed slopes. Black points are median estimates. Thick and thin gray lines are the 50% and 95% credible intervals, respectively. The seven streams presented in Figure 3.1 are labeled.

Chapter 4. Fisheries portfolio diversification and turnover buffer Alaskan fishing communities from abrupt resource and market changes[1]

4.1 ABSTRACT

Abrupt shifts in natural resources and their markets are a ubiquitous challenge to human communities. Building resilient social-ecological systems requires approaches that are robust to uncertainty and to regime shifts. Harvesting diverse portfolios of natural resources and adapting portfolios in response to change could stabilize economies reliant on natural resources and their markets, both of which are prone to unpredictable shifts. Here we use fisheries catch and revenue data from Alaskan fishing communities over 34 years to test whether diversification and turnover in the composition of fishing opportunities increased economic stability during major ocean and market regime shifts in 1989. More than 85% of communities show reduced fishing revenues following these regime shifts. However, communities with the highest portfolio diversity and those that could opportunistically shift the composition of resources they harvest, experienced negligible or even positive changes in revenue. Maintaining diversity in economic opportunities and enabling turnover facilitates sustainability of communities reliant on renewable resources facing uncertain futures.[1]

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4.2 INTRODUCTION

Ecosystem dynamics are notoriously unpredictable, especially considering the effects of ongoing climate change, ocean acidification, and other poorly understood and interacting perturbations. It is often argued that more mechanistic science will lead to greater understanding of ecosystem functioning and improved forecasting for variability and change (Travis *et al.* 2014). As such, there has been tremendous scientific effort to forecast and anticipate approaching regime shifts (Scheffer *et al.* 2009), yet the utility of these approaches is often challenged in real-world applications (Boettiger and Hastings 2013). Our ability to accurately predict the timing and character of changes in ecosystems and populations will always be limited; thus, there is distinct need to develop strategies to promote ecological and socio-economic resilience without reliance on accurate long-term forecasts (Schindler and Hilborn 2015).

A large proportion of the world's population lives in coastal communities and is critically dependent on highly volatile marine resources (Adger 2000). Fisheries are highly variable and risky as an income source (Kasperski and Holland 2013) as the populations they depend on fluctuate strongly at interannual and interdecadal time scales (Steele 1998, Vert-pre *et al.* 2013). Additionally, fisheries are coupled social-ecological systems that are affected not only by biological responses to oceanographic changes, but also by socio-economic conditions and market demand expressed at local to global scales (Clark 1981). For example, prices paid to fishermen can be highly volatile and may easily double or halve from year to year, depending on global market conditions (Knapp 2007). Communities that rely on fisheries, or most natural renewable resources, for their livelihoods need to integrate over variability, shocks, and reorganization of the integrated social-ecological system to sustain their economies and livelihoods (Allison and Ellis 2001). The capacity of coupled human-natural systems to reorganize through turnover in composition while maintaining key functions in response to a changing environment is a hallmark of the resilience concept (Holling 2001, Walter *et al.* 2004, Folke *et al.* 2010). There is a pressing need to understand what factors enable resilience and potential for adaptation in social-ecological systems against new climate realities and globalized economies (Österblom et al. 2016).

Forecasting and insurance are two strategies that have been used extensively to help buffer people against unexpected perturbations to natural resource economies; the former is used to avoid risks while the latter is used to transfer damages from negative perturbations (Sethi 2010). In financial markets, investors use portfolio diversification to buffer against risk when forecasts have little power (Markowitz 1952). Investors also use turnover, the buying and selling of different assets, to adapt to shifting markets and exploit emerging opportunities. These concepts have a rich history in economic and biodiversity theory (Tilman *et al.* 1996) and the range of benefits continues to become apparent (Margurran 2016). Portfolio diversification, in terms of exploiting multiple species or populations, has been shown to stabilize interannual variability in commercial fisheries and fishing communities (Holling 2001, Worm *et al.* 2006, Schindler *et al.* 2010, Kasperski and Holland 2013, Sethi *et al.* 2014). However, it remains unclear whether diversification or adaptation through turnover of opportunities (Aguilera *et al.* 2015) can provide resilience for communities in the face of large and abrupt regime shifts.

Abrupt shifts in ecosystems and fish stocks are common in the marine environment (Steele 1998, Vert-pre *et al.* 2013). Importantly, these regime shifts can have major economic consequences as biological communities reorganize in response to ecosystem and ocean dynamics (Steele 1998, Hare and Mantua 2000). Regime shifts are also present in markets for natural resources (Knapp 2007, Naylor *et al.* 2000, Asche *et al.* 2013). For example, Pacific salmon have shown abrupt and persistent changes in their market price due to fluctuations in global aquaculture production of salmon (Knapp 2007). Diversification (the distribution of participation across a number of fisheries), and turnover (reorganization of fishing effort among fisheries to capitalize on emerging opportunities), should alleviate economic hardships and provide resilience in the face of large and abrupt regime shifts. While the concepts of diversification and turnover have been considered key components of social-ecological resilience in a theoretical sense (Walker *et al.* 2004 Folke *et al.* 2010) and in small-scale fisheries (Aguilera *et al.* 2015), the magnitude of their effects on the resilience of social-ecological systems against regime shifts has yet to be quantified at a large scale with empirical data.

Here we use a well-documented oceanographic regime shift with far reaching biological consequences in the North Pacific Ocean (Hare and Mantua 2000, Benson and Trites 2002), and a global market regime shift in the price of salmon (Knapp 2007), to test the hypothesis that diversifying fishing opportunities and enabling turnover in the composition of what is harvested provide resilience against abrupt shifts for fishery-dependent communities. We used data from Alaska where many communities are intimately tied to fishing for their livelihoods and where commercial catches and revenues have been fully monitored over three decades. We focus at the scale of communities because many of the socio-economic benefits of resilience are expressed at the community scale. For example, many Alaskan communities derive much of their tax revenue from fishery landings, fishing activity generates other commerce within the community, and their social identity is often expressed at the community scale (Holen 2014). Additionally, there exists a natural gradient in diversification among communities driven by geographic isolation and economic opportunity that provides contrast for comparison. These data comprise more than 60 fisheries, 100 individual communities, and thousands of permit holders all susceptible to abrupt shifts in the resources and markets.

Our results show that diversification and turnover of fishing opportunities significantly reduce the negative impacts of regime shifts on the revenues generated by fishing communities. We find that more than 85% of fishing communities saw large decreases in their revenues following major ocean regime and market shifts. However, communities that participated in a more diverse collection of fisheries saw smaller changes in revenue and had more opportunities to adapt to the changes. In some cases, communities actually increased their revenue from fishing as they were able to capitalize on emerging opportunities. Enabling communities to create and maintain flexibility in fishing opportunities appears to be a tangible mechanism for providing resilience against unpredictable changes in ecosystems and markets. Building sustainable communities will require employing strategies that are robust to irreducible uncertainties about future changes in coupled human-natural systems.

4.3 RESULTS

Ocean regime shift reorganizes commercial fisheries catch

The ecosystems of the North Pacific Ocean are notoriously variable, expressing change at interannual and interdecadal time scales large enough to seriously challenge the sustainability of fishery-dependent communities. These unpredictable changes in productivity and species composition are due mostly to oceanographic changes that favor certain stocks or species. Importantly, these changes do not result in the unilateral collapse or benefit of all species; rather they cause a reshuffling of the relative abundances of important commercial species (Hare and Mantua 2000). It has been well documented that, in 1989, there were major changes in productivity and species composition across the North Pacific that have persisted since the regime shift (Hare and Mantua; Figure 4.1 A). There were observed changes in recruitment of many species (Hare and Mantua 2000, Benson and Trites 2002). Oceanographic changes are most likely to impact juvenile fishes and recruitment (Hare and Mantua 2000, Benson and Trites 2002); therefore, the timing of changes in adult stock size and impacts on fisheries will be dependent on the life-history of the species and age they recruit to the fishery (Noakes and Beamish 2009).

To understand how the 1989 regime shift affected commercial fisheries across Alaska, we evaluated changes over time in commercial fisheries harvest by stock. Using dynamic factor analysis (Zuur *et al.* 2003), a dimension reduction technique developed specifically for time series, we searched for the most common shared trend among time series of commercial catches from 60 different fish stocks harvested throughout Alaska (Figure 4.1 B, Supplementary Table 1). The dominant pattern in commercial fisheries catch shared among stocks shows striking changes around 1989 indicating the influence of the regime shift on fishery catches (Figure 4.1 B). However, not all stocks or species responded in the same direction (Figure 4.1 B inset). While total pounds harvested in Alaskan fisheries increased by about 30% after 1989, many stocks (66%) exhibit a negative response to the changes in ocean conditions after 1989 (Figure 4.1 B inset). Notably, stocks of salmon and herring in the northern Bering Sea declined after 1989, but catches of walleye pollock and salmon in Southeast Alaska increased. How these shifts in the composition of commercially available species manifest as changes in revenue for resource-dependent communities is likely mediated by the exploitation strategies or constraints on individual communities.

Ocean regime and market shifts impact fishing revenues

To understand the impacts of the regime shift and changes in commercial fishery harvest on Alaskan fishing communities, we evaluated the trends in commercial fishing revenue which also changed substantially after the 1989 regime shift (Figure 4.1 C,D). We again used dynamic factor analysis on revenue time series for 105 Alaskan fishing communities, based on ex-vessel values, to reveal common trends in revenue that were shared among Alaska's fishing communities (Figure 4.1 C,D). There was model support for two independent trends in revenue over time (Supplementary Table 2), both of which indicate significant changes in revenue derived from commercial fishing, but for different reasons. The first shared trend is highly correlated (r=0.86, Pearson correlation) with the common trend in commercial catches (Figure 4.1 B). The second shared trend is highly correlated (r=0.87, Pearson correlation) with the price-per-pound paid to fishers for Pacific salmon species, the dominant commercial fisheries by value in Alaska (Figure 4.1 C). There are obvious feedbacks between catch and price as supply and demand relationships have strong influence on the value of fisheries (Clark 1981); however, this change in salmon price was driven primarily by a substantial increase in global aquaculture production of salmon (Knapp 2007). While changes in catch or price alone can generate strong changes in revenue, synergistically they can influence revenue with no absolute change in either one. Simply changing the composition of catch among the different relative values can significantly impact revenue. Here we find that changes in revenue are significantly controlled by changes in catch, price, and the product of the two (Supplementary Table 3).

Diversity of fishing among Alaskan fishing communities

A gradient in the diversity of fishing opportunities exists across Alaskan fishing communities that is driven by demographic and geographic patterns. Commercial fishing in Alaska is a vital source of income statewide providing \$1.3 billion annually from harvest alone (NMFS 2010), and in some remote areas where other sources of income are scarce, fishing may be the only major industry (Knapp 2011). Despite the clear importance of fishing and the risks associated with fishing as an income source (Kasperski and Holland 2013), many communities participate in only a few fisheries (Figure 4.2). In more developed regions, which have more access to capital or a higher diversity of commercial fish stocks nearby, communities often participate in 30 or more fisheries distributed across several species. Many communities participate in a similar group of fisheries, but few have their efforts broadly distributed across those fisheries (Figure 4.2). Both the number of fisheries a community participates in and distribution among these (evenness) are potentially important dimensions of diversity and its role in stabilizing community revenues.

Diversity and turnover provide resilience against regime changes

To measure the effect of diversification of fishing opportunities in creating resilient communities, we compared changes in revenue in response to the regime shifts against the degree of diversification in fishing communities across Alaska. Overall, 93 of 105 communities showed decreased fishing revenue following the 1989 regime shift and abrupt change in price, but the magnitude of the response was strongly modulated by diversity in the composition of each community's revenue (Figure 4.3 A). We compared the average revenue in the 10 years prior to 1989 with the average revenue in the 10 years following, and related the percent change in revenue with each community's level of diversification across species and locations prior to the regime shift (Figure 4.3 A). Many communities lost more than 50 percent of their revenue following the 1989 regime shifts. Others saw large increases. Communities that participated in, and had revenue spread across a broader suite of fisheries showed smaller losses in revenue in response to the ecological and market changes that occurred in 1989 (Figure 4.3 A). Communities with the highest levels of diversity saw little or no change in revenue. In aggregate, fishery revenues statewide declined by about 15%; therefore, a more diversified approach for many small communities could have reduced their revenue losses. An important aspect of this log-linear relationship is that a relatively small level of diversity, a value of approximately three (reciprocal Simpson's index), provides most of the benefit of diversification (Figure 4.3 A). Yet more than 80 percent of communities fall below three and most are below two. For context, this value could correspond to a strategy with three fisheries evenly divided or a dominant fishery with several smaller supporting fisheries. Here, a more even distribution among fisheries provided a greater benefit than the number of fisheries alone (Supplementary Table 4). One of the major requirements for diversity to enhance stability is that components vary asynchronously. Simply diversifying among three similar species or across small spatial scales may not necessarily improve resilience.

A second consequence of this log-linear relationship is that further increases in diversity may have diminishing returns. There is a need for more explicit assessments of how to distribute risk by constructing efficient resource portfolios in resource-dependent communities. Diversification of fishing opportunities, in this coupled human-natural system, substantially reduced the vulnerability of fisheries revenues into communities against these regime shifts, demonstrating the potential for resource heterogeneity to ameliorate risk to future abrupt changes in ecosystems and markets.

A major consequence of the 1989 regime shift was complementary changes in species abundance (Benson and Trites 2002), where some species increased in abundance as others showed marked declines. We measured turnover, the relative change in the composition of a community's catches, within each community's fishing portfolio from before to after 1989 using Jaccard's dissimilarity index. Together with diversification, turnover explained 26% of the variation in changes in community revenue including a significant interaction (Figure 4.3 B, Supplementary Tables 5 and 6). Communities with the highest diversity had higher turnover while communities with small diversity had little or no turnover. Having a diverse portfolio of fishing opportunities and the ability to shift the relative distribution of stocks within the portfolio improved changes in revenue and in fact enabled some communities to increase revenue streams from fishing despite substantial shifts in abundance, species composition, and prices (Figure 4.3 B). While only a small level of diversity reduces vulnerability, having a large set of fishing options provides opportunity to more easily adapt to and take advantage of fluctuations in species abundance and prices. Creating and maintaining flexibility in fishing opportunities appears to be an effective tool for providing resilience against unforeseen changes in environmental and economic conditions.

4.4 DISCUSSION

Diversification has long been a critical attribute of traditional fishing economies (Allison and Ellis 2001). For subsistence fishing communities around the North Pacific, salmon have often been the core of their economies, but intertidal shellfish, and marine fish and marine mammals were often important, especially when salmon returns were low (Glavin 2000). Recognizing the tendency of open-access fisheries to develop too many fishing boats, and in response to depleted fish stocks, ‘limited entry’ was introduced, which has reduced access for many people and forced specialization for efficiency. As access to fisheries is limited, buying into additional fisheries can be difficult and costly. However, the results presented here suggest that such investments likely have substantial long-term benefits to communities.

Diversification has clear benefits to fishing communities, but it can be challenging to achieve. Key limitations, especially for small communities, are access to capital to purchase fishing rights and permits, and to develop capacity for processing seafood products, and physical access to a wide array of fishing resources. Not all Alaskan stocks are fully exploited and rights for many fisheries can be purchased in markets, yet these fishing permits and rights can be prohibitively expensive. For example, permits for access to some Alaskan salmon fishing opportunities can be in excess of $300,000 (USD). In Alaska, we see patterns of diversification that follow geographic access to resources as well as economic development (Figure 4.2). Communities in Southeast Alaska where diverse fishing opportunities exist in close proximity had the highest levels of diversity. Importantly, the small level of diversity needed to mitigate most of the risk in this social-ecological system (due to the log-linear relationship) could markedly reduce these barriers to diversification.

Diversification also carries risks such as loss of efficiency due to lack of specific knowledge as well as high capital costs. Diversification has been mostly thought of as an individual level strategy (Kasperski and Holland 2013) not a community one, therefore a community’s ability to influence diversification has been limited. Yet, fishing by individuals provides a vital revenue stream into communities, which supports many other supporting industries through commerce as well as infrastructure through taxes. Importantly, the constraints on community diversification are likely to be different than those on individuals. There are often legal restrictions that may prevent individuals from owning diverse fishing rights. High capital costs, which may be prohibitive for individuals, could be reduced within communities through directed efforts such as permit pooling or lease programs. For example, Alaska Native Corporations or economic development organizations (organizations whose goals are to improve the economic standing of native Alaskans and specific regions within the state) currently use some of their resources to help people become more competitive in specific fisheries. An alternative strategy could be to use resources to help communities with limited access to capital gain more diverse fishing opportunities. Could communities circumvent some of the loss in efficiency by distributing specialist fishers among diverse opportunities, rather than having many diverse individuals? The benefits of diversification are clear and fishing dependent communities need policies and potentially novel practices that enable opportunities and encourage diversification and flexibility.

Over the last decade, there has been considerable interest and effort toward implementing ecosystem-based fisheries management under which multiple objectives and stakeholders, rather than single species, are considered in the management of fishing sectors and ecosystems (Pikitch *et al.* 2004). Diversification lends itself nicely to an approach that calls for exploitation distributed across ecosystem components (Garcia *et al.* 2012) while creating important buffers against variability and regime shifts. This approach may also have ecosystem benefits. As some stocks get smaller and the costs of harvest increase, switching among fishing opportunities to more abundant stocks may reduce pressure on stocks in decline.

Here we show that diversification and the ability to opportunistically shift the composition of species exploited can buffer communities against unexpected and large-scale ocean regime shifts and changing markets. Ecosystems can undergo significant shifts in composition, but often maintain their overall productivity. While delivery of ecosystem services is provided primarily by abundant species (Winfree *et al.* 2015), the species that are abundant now may not be in the future. Additionally, species that have small market share now may demand premium prices in the future. Diversification provides opportunities to take advantage of emerging changes and buffers against disaster; it is a tangible means to increase the resilience and adaptive capacity of coupled human-natural systems. Due to the immense complexity of the ecosystems, markets, and the feedbacks between them, we will always have limited scientific capacity to anticipate future changes. Thus, there is critical need to employ strategies that enable sustainable communities despite deep and irreducible uncertainty about the future conditions of the coupled human-natural system they depend on.

4.5 METHODS

Data

The state of Alaska manages all fisheries operating within 3 nautical miles of shore and a small set of fisheries operating in the US exclusive economic zones (> 3 nautical miles). Alaskan commercial fisheries are delineated by taxa (either species or species group), the area harvested, and the gear used to harvest them. State managed fisheries are mostly managed using some form of limited entry where access is controlled, but can be bought or sold among parties. Any individual harvesting in a state managed fishery requires a permit specific to the taxa, area fished, and gear used. All landed catches and revenue in Alaskan commercial fisheries are required to be reported. The CFEC tracks landings and revenue by permit and permit-holder residency. Therefore, reported catch and revenue are assigned to communities where the permit holder resides. For confidentiality reasons, the CFEC cannot report very small fisheries that have less that 4 permit holders per community. Therefore these fisheries are not included in our analysis. Management of sablefish and halibut fisheries switched to individual transferable quota systems in 1995, which could alter the revenue and catches in these fisheries. However, excluding catches and revenues for these species does not change the results in this study.

We used community level gross fishing revenues data collated by the CFEC. These revenues represent the sum of annual gross fishing revenues attributable to CFEC commercial fishing permits registered to a specific Alaskan community. Some communities have seen changes and permit migration. We ran these analyses using revenue per permit fished to account for these changes, and there is no change in the results or conclusions. All revenue data were adjusted for inflation to 2013 USD using the US annual average consumer price index (http://www.bls.gov/cpi/). To evaluate spatial patterns in diversification we used revenue data aggregated to US census areas (Figure 4.2). Population and demographic information by census area were taken from U.S. 2010 census data (www.census.gov). Salmon price data was provided by CFEC summary data. Prices were adjusted for inflation to 2013 USD using the US annual average consumer price index.

Analysis

To search for common trends in commercial fisheries catch among different stocks across Alaska as well as common patterns in community revenues we applied dynamic factor analysis (Zuur *et al.* 2003; DFA) to time series of commercial harvest by stock and to time series of Alaskan fishing community revenue (separate analyses). Similar to principal component analysis, DFA is a dimension reduction technique designed specifically for use with time series data. With DFA, we are trying to explain temporal variation in a set of *n* observed time series using linear combinations of independent hidden random walks. The model structure is as follows:

The state equation of a vector of common random walk trends over time:

$$\boldsymbol{x}_t = \boldsymbol{x}_{t-1} + \boldsymbol{w}_t \qquad \boldsymbol{w}_t \sim MVN(0, \boldsymbol{Q}) \tag{1}$$

Observation equation relates trend ($\boldsymbol{x}$) to observations ($\boldsymbol{y}$).

$$\boldsymbol{y}_t = \boldsymbol{Z}\boldsymbol{x}_t + \boldsymbol{v}_t \qquad \boldsymbol{v}_t \sim MVN(0, \boldsymbol{R}) \tag{2}$$

Here, the vector of observations for catches in each stock (or revenue in each community) at time *t* ($\boldsymbol{y}_t$) are modeled as linear combinations of hidden trend ($\boldsymbol{x}_t$) and factor loadings on the hidden trend for each stock (community) ($\boldsymbol{Z}$). $\boldsymbol{v}_t$ and w_t represent the observation and process error structures respectively. To make the model estimable[24] process error (**Q**) was set to a diagonal matrix of value 1. Observation errors (**R**) are from a multivariate normal distribution. The number of trends and the error structure are determined through model selection. Candidate models were compared using AIC based on the maximum likelihood of the model fit. Model selection results for DFA analyses are in Supplementary Tables 1 and 2.

To evaluate common trends in commercial fisheries harvest among stocks around Alaska we applied the DFA to time series of fisheries delineated by taxa and location harvest (i.e. catch was aggregated among different gear types within the same taxa/location combination). This yielded an increased number of complete time series of catch. We limited stocks to only those that had no more than three zero-catch values (n=60). This increased the overall diversity of taxa and locations represented in the data. We compared models with one or two hidden trends as well as two error structures; where all stocks share a single observation error (diagonal and equal) and where all stocks have individual observation error (diagonal and unequal). All data were z-scored to account for differences in means and intrinsic variance dynamics.

In a separate analysis we applied the DFA to time series of fishing community revenues allocated to Alaskan cities. For fishing communities we included only those that had non-zero revenue in all years between 1980 and 1999 (n=105). We compared models with 1 or 2 hidden trends as well as two error structures; where all stocks share a single observation error (diagonal and equal) and where all stocks have individual observation error (diagonal and unequal). All data were z-scored to account for differences in means and intrinsic variance dynamics. DFA models were fit using the 'MARSS' package in R (Holmes *et al.* 2013).

To measure the effect of diversification on changes in community revenues and commercial fishing catches we compared revenue and catch before and after 1989 and diversity in fishing opportunities as well as turnover. We included only communities with non-zero revenue in all years between 1980-1999. Shifts in revenue were simply computed as the percent change in the mean annual revenue for the period 1980-1989 and the period 1990-1999 allocated to individual communities. Changes in catches were computed this same way using total annual pounds landed allocated to individual communities. The earliest available year for catch and revenue data reported to individual communities is 1980 (total of 10 years pre-regime shift). For an even comparison we used only the 10 years post-1989 (1990-1999).

Diversity was computed for each community over the 10 years prior to the 1989 (1980-1989). We used the reciprocal Simpson's index (1/D) where diversity (D)

$$D = \sum_i {p_i}^2 \tag{3}$$

where p_i is the proportion of total revenue by fisheries (taxa and location). To compute an overall diversity metric for each community we weighted each year by the relative proportion of that year to the total revenue for all years.

To measure turnover in the relative composition of a community's commercial fishing catches, we compared the commercial fisheries catches from before and after 1989. For each community a relative composition by fishery was computed based catches on for each of two periods, 1980-1989 and 1990-1999. Specifically, each fishery's contribution to the total catch for each period in total was computed. Then, the relative change in composition was computed using Jaccard's dissimilarity (J) index between these two time periods, A (1980-1989) and B (1990-1999).

$$J = \frac{|A \cup B| - |A \cap B|}{|A \cup B|} \tag{4}$$

All diversity and turnover metrics were computed in R using the 'vegan' package (R Core Team 2014).

We compared relationships between changes in revenue and diversity and turnover using linear regression. To assess the relative strength of the two types of diversity and their interaction we computed effect sizes using z-score standardized covariates.

Data availability statement:

The fisheries data that support the findings of this study are publically available online from the Commercial Fisheries Entry Commission (CFEC).

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4.7 FIGURES

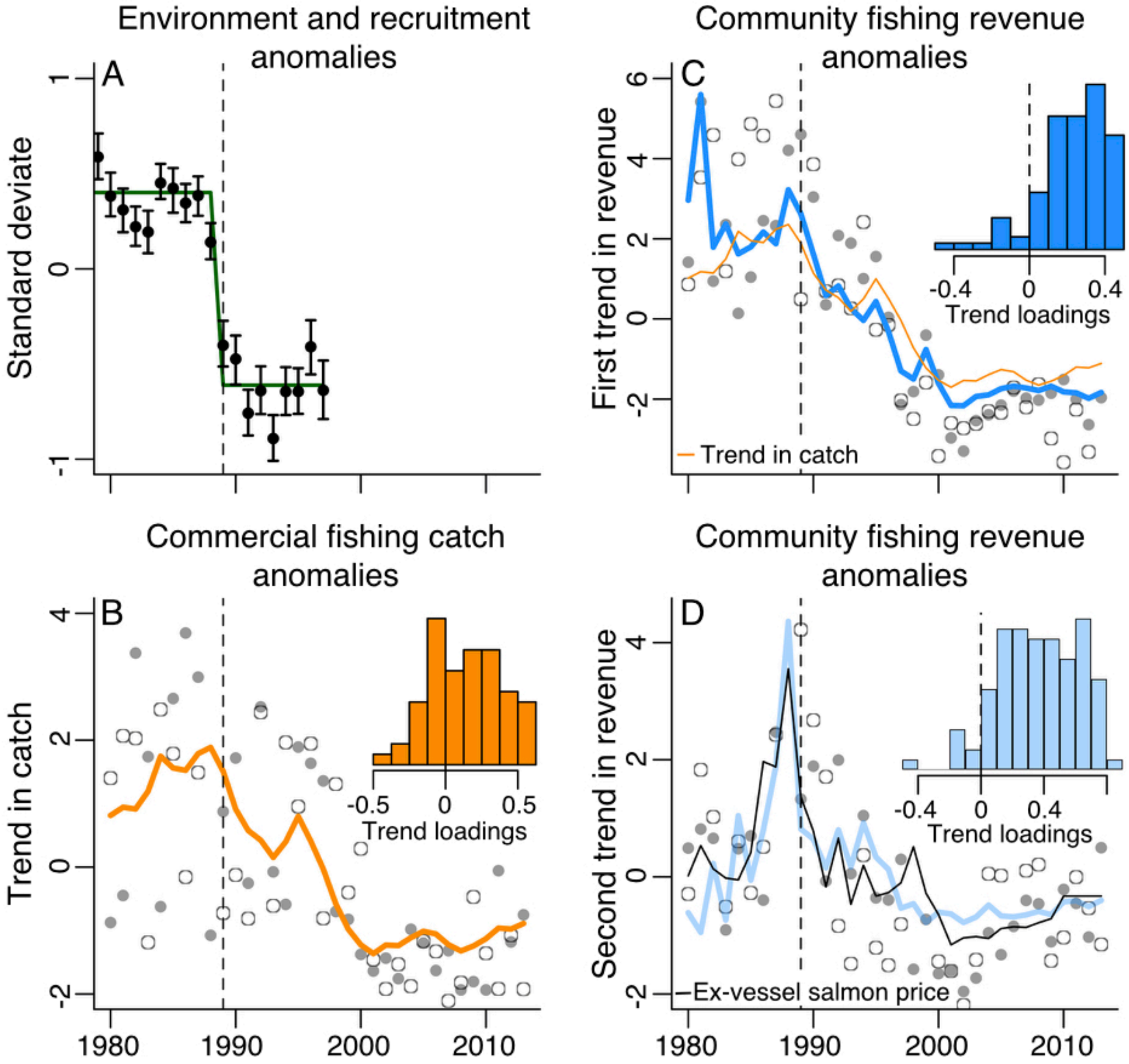


Figure 4.1: Ocean regime changes and market shifts impact fisheries catch and revenue A) Regime shift analysis of 100 physical, chemical, and biological time series from across the North Pacific region (redrawn from Hare and Mantua 2000). The green line represents the average deviate from before and after 1989; B) The most commonly shared trend in commercial harvest by stock (species location combinations) (orange line) as determined by dynamic factor analysis

(DFA). The analysis included time series of commercial harvest from 60 stocks delineated by fishery group (e.g. crab, salmon) and location harvested (e.g., Prince William Sound, Southeast). Open and closed circles in gray are example fits for two stocks. Inset histogram of factor loadings of individual stocks on the shared trend in commercial catches. Loadings indicate the strength of association between the commercial catch of a stock and the estimated trend. A negative loading indicates that the commercial catch of a stock trends in the opposite direction. C.) The first of two commonly shared trends in commercial fishing revenue across communities in Alaska as determined from a DFA (blue line). The analysis included time series of commercial fishing revenue from 105 communities from across Alaska. The orange dashed line is the common trend in commercial fisheries catches by stock (panel B). Open and closed circles in gray are example fits for two communities that loaded strongly on the first trend. Inset histogram of factor loadings of individual fishing communities on the first shared trend in commercial fishing revenue. D.) The second of two commonly shared trends in commercial fishing revenue (blue line). Open and closed circles in gray are example fits for two communities that loaded strongly on the second trend. The black line indicates the real ex-vessel price per pound for salmon paid to fishers in Alaska. Price is z-score standardized for display on the same axes. All price and revenue data were adjusted for inflation using the consumer price index (2013 US$). Inset histogram of factor loadings of individual fishing communities on the second shared trend. The vertical dashed line in all panels marks 1989 and indicates the timing of the regime shifts.

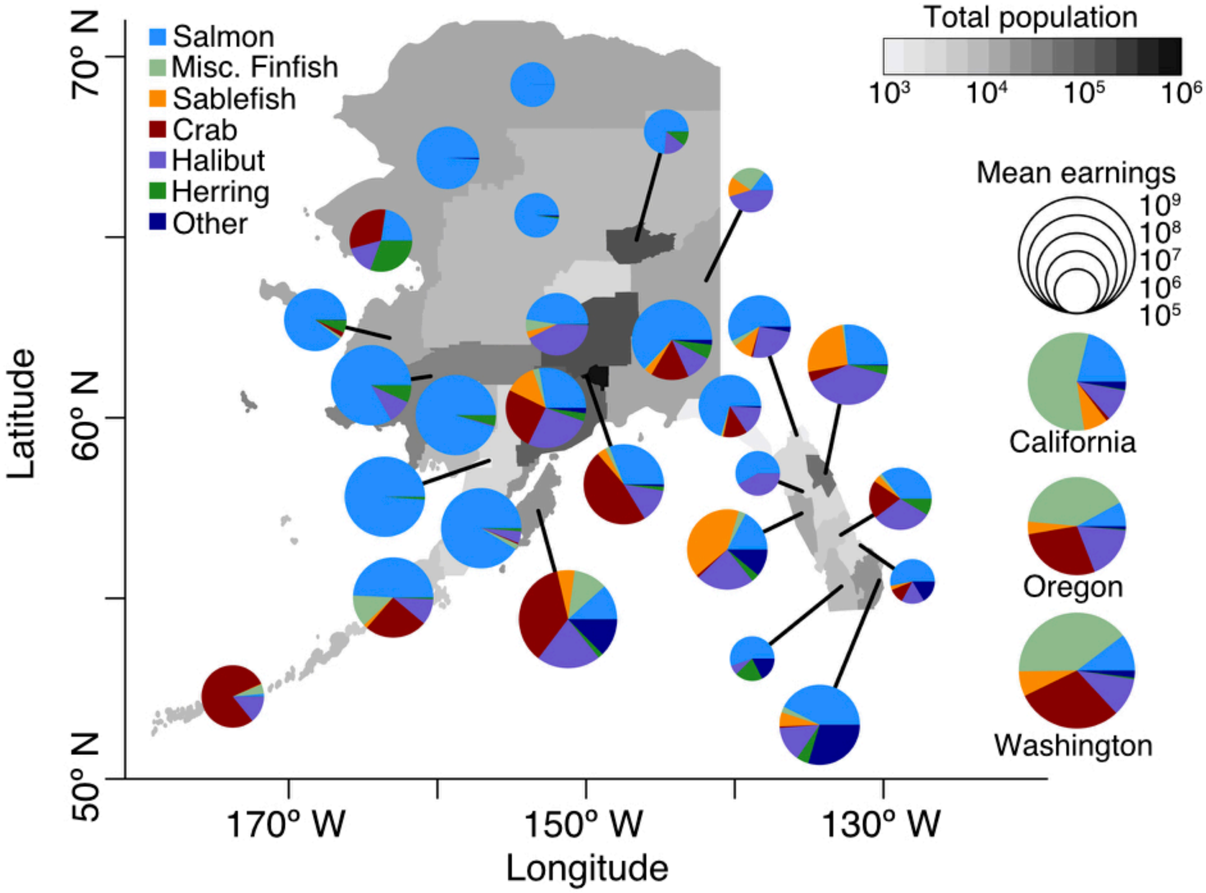


Figure 4.2: Variation in diversification of fishing opportunities across Alaskan communities Average revenues from the largest six major species/groups in Alaska from 1980-2013 are aggregated by census area or borough. Pie chart diameter reflects the average annual revenue (mean earnings) from fishing in 2013 US dollars. Graphs for California, Oregon, and Washington are for revenue from Alaskan state fisheries by permit holders residing in those states. Revenue is allocated to permit holder residence, not fishing area.

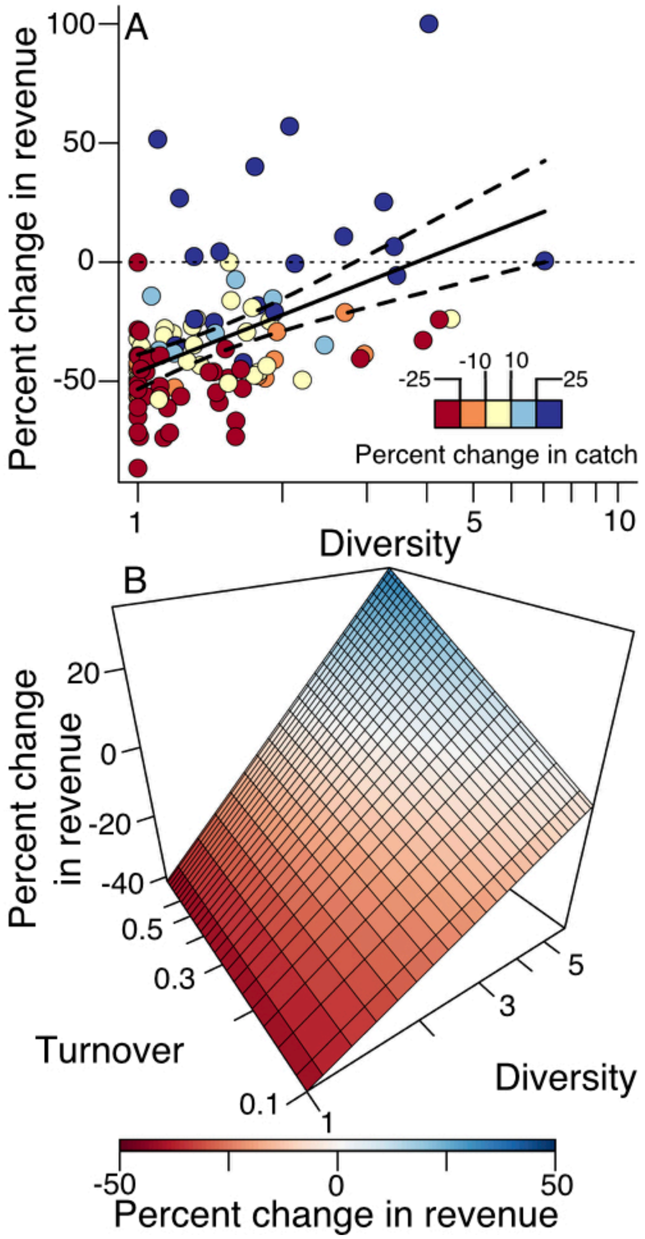


Figure 4.3. Diversification and turnover of fishing opportunities buffer against abrupt shifts A.) Observed changes in revenue from before (1980-1989) and after (1990-1999) the regime shifts are plotted against diversity of fishing opportunities for 105 Alaskan fishing communities. Diversity, plotted on a log-scale, was measured as the reciprocal Simpson's index so increasing values are increases in diversity. Diversity indicates both the total number of opportunities and the distribution among component stocks. Diversity is computed for each community over the 10

years prior to 1989. Total annual revenue from fishing (2013 US dollars) were used to weight years in the computation of the diversity index. The line of best fit with 95% confidence intervals is plotted in black (R^2=0.21, p<0.001, linear regression). Percent change in commercial fishing catch is represented by the color gradient, with cool colors representing a positive percent change and warm colors a negative percent change. B.) Wireframe of the percent change in revenue against diversity and turnover. Turnover (often referred to as beta diversity) is Jaccard's dissimilarity index measuring changes in the in the relative contribution of stocks to a communities overall portfolio (by catch). Turnover is plotted on a log scale but values range from zero turnover to 0.4 or 40% turnover, with increasing turnover towards the back of the plot. The wireframe is generated from predictions of a linear model between diversity and turnover including a significant interaction (R^2=0.26, p<0.0001, linear regression, Supplementary Tables 5 and 6). Ranges used to generate the surface are well within the bounds of the data as to produce conservative changes in revenue within the bounds of the observed data (Supplementary Fig. 1).

Appendix A: Supplementary material for Chapter 1

Supplementary Table 1: Dynamic factor analysis model selection results for models of the change in the proportion of sockeye salmon spending one year in freshwater. All models include one shared common trend and an ‘unconstrained’ error matrix to account for shared variation among systems. (LakeTemp = Lake Aleknagik average summer lake temperature, IceOff = day of spring ice breakup on Lake Aleknagik, Esc = system specific escapement values used as an index of juvenile density and competition, PDO = Pacific Decadal Oscillation, NPGO = North Pacific Gyre Oscillation)

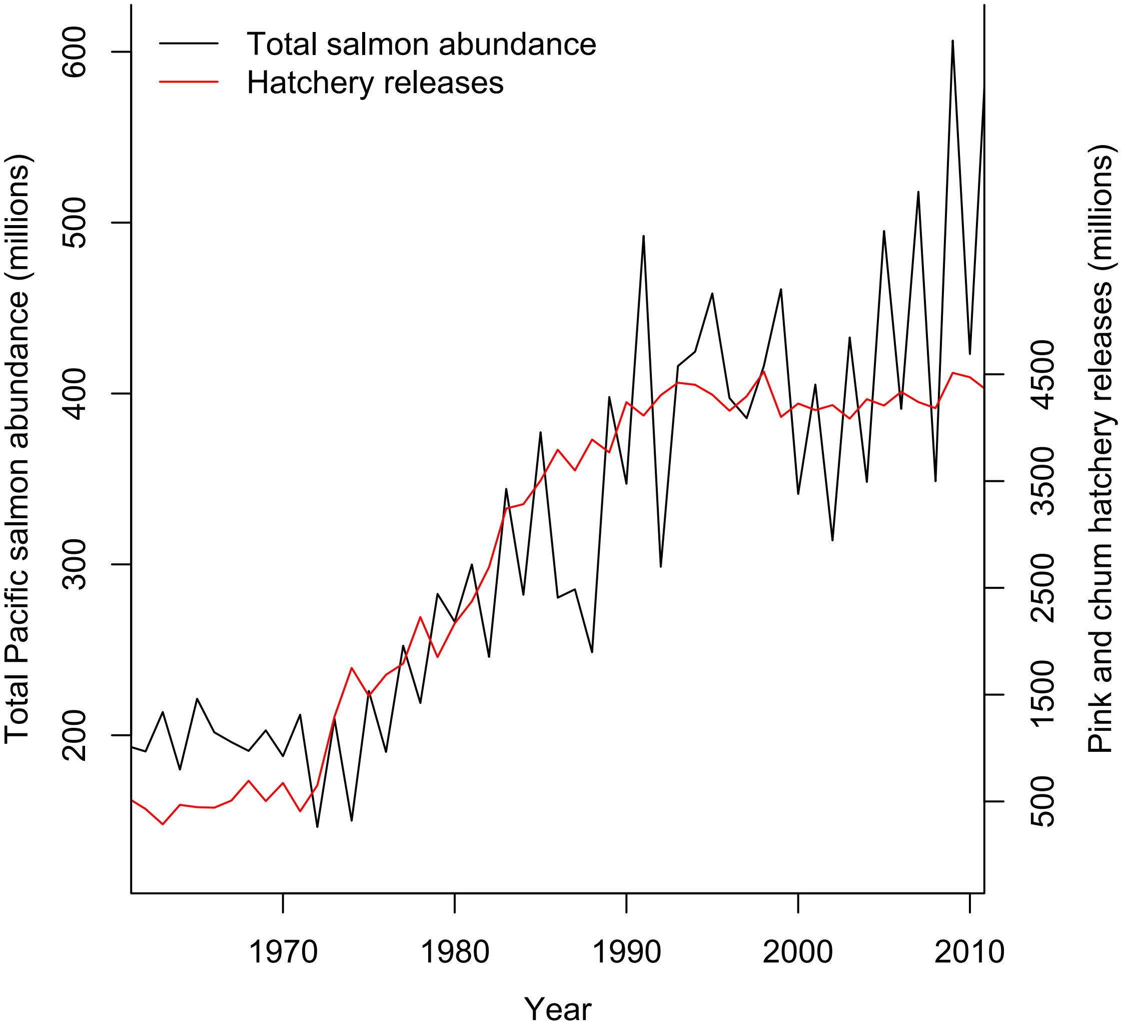
Model	Num. Parameters	-logLik	AIC	ΔAIC
LakeTemp	**42**	**308.9**	**701.7**	**--**
Esc + LakeTemp	49	304.9	707.8	6.1
IceOff	42	313.4	710.7	9.0
PDO	42	314.3	712.5	10.8
Esc + PDO	49	308.5	715.0	13.2
Esc + IceOff	49	308.6	715.1	13.4
--	35	325.1	720.1	18.4
Esc	42	320.9	725.8	24.1
NPGO	42	323.1	730.2	28.5
Esc + NPGO	49	318.9	735.8	34.0

Supplementary Table 2: Dynamic factor analysis model selection results for models of the change in the proportion of sockeye salmon spending three years in the ocean. All models include one shared common trend and an 'unconstrained' error matrix to account for shared variation among systems. (PROP1= district specific proportion of sockeye that spent 1 year in freshwater by brood year, PDO=Pacific Decadal Oscillation, NPGO = North Pacific Gyre Oscillation, Stocking = number of hatchery released pink and chum salmon)

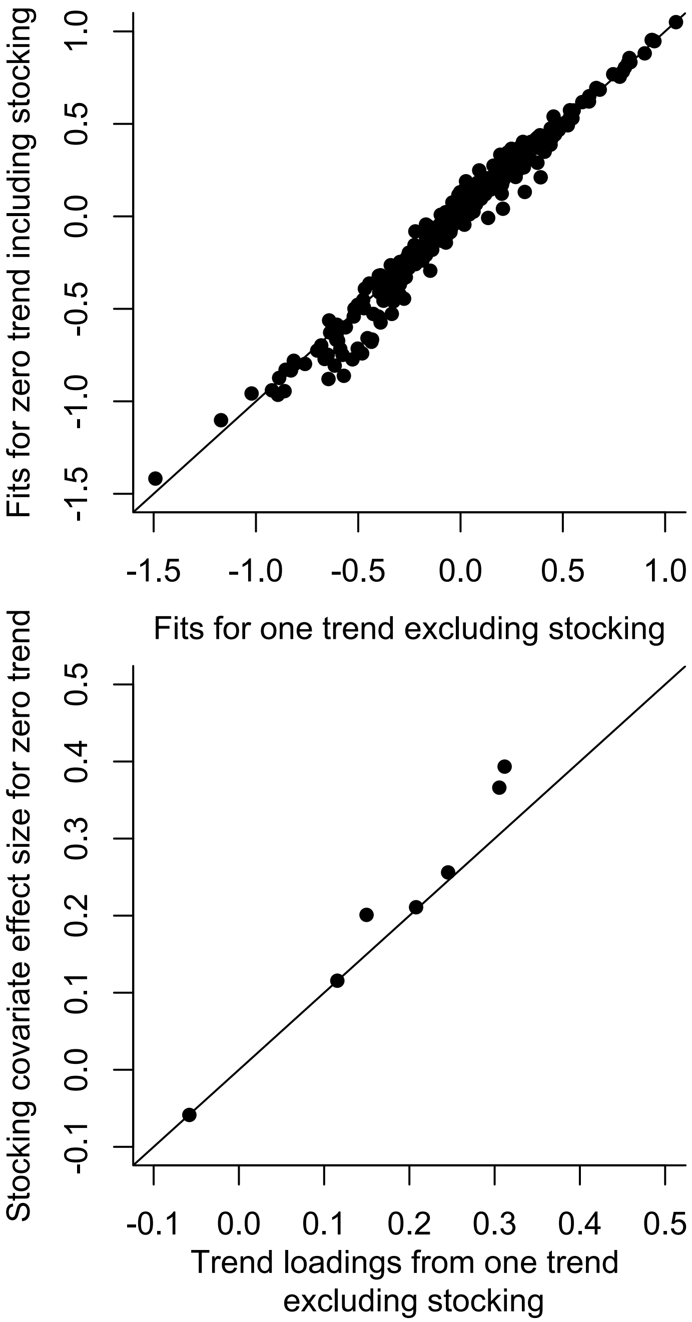
Model	Num. Parameters	-logLik	AIC	ΔAIC
PROP1	**42**	**363.9**	**811.8**	**--**
PROP1+ PDO	49	357.4	812.8	1.0
PROP1+ NPGO	49	359.9	817.7	5.9
No covariates	35	374.5	818.9	7.1
PDO	42	370.0	823.9	12.1
NPGO	42	370.0	824.0	12.2
Model with no latent trend				
No latent trend + PROP1 + Stocking	42	361.0	806.1	--

Supplementary Table 3: Dynamic factor analysis model selection results testing for the influence of exploitation rate on the change in the proportion of sockeye salmon spending three years in the ocean. All models include one shared common trend and an ‘unconstrained’ error matrix to account for shared variation among systems. (PROP1= district specific proportion of sockeye that spent 1 year in freshwater by brood year, ER0, ER1, and ER2 = fishing district specific exploitation rates lagged by 0,1, and 2 generations respectively). To for fishery selection for a lag of two generations, observation time series had to be shortened by the length of one generation, therefore AIC is only directly comparable to the shortened model including PROP1.

Model	Num. Parameters	-logLik	AIC	ΔAIC
PROP1	**42**	**363.9**	**811.8**	**--**
PROP1+ ER1	49	358.8	815.6	3.8
PROP1+ ER0	49	360.2	818.3	6.5
Models with shortened time series to allow for two generations				
PROP1	**42**	**316.4**	**716.9**	**--**
PROP1 + ER2	49	313.0	723.9	7.0



Supplementary Figure 1: Trends in total Pacific salmon abundance and pink and chum salmon hatchery releases at the scale of the North Pacific Ocean. Data available from the North Pacific Anadromous Fish Commission (www.npafc.org).



Supplementary Figure 2: Model fit comparison between a DFA model including 1 latent trend and the proportion of sockeye spending one year in freshwater and a model with no latent trend but including the proportion of sockeye spending one year in freshwater and the number of hatchery releases of pink and chum salmon into the North Pacific. (Top panel) Comparison of model fits between the two models. Diagonal line is the 1:1 line. (Bottom panel) Comparison of parameter estimates for the effect of stocking between the two models. Diagonal line is the 1:1 line.

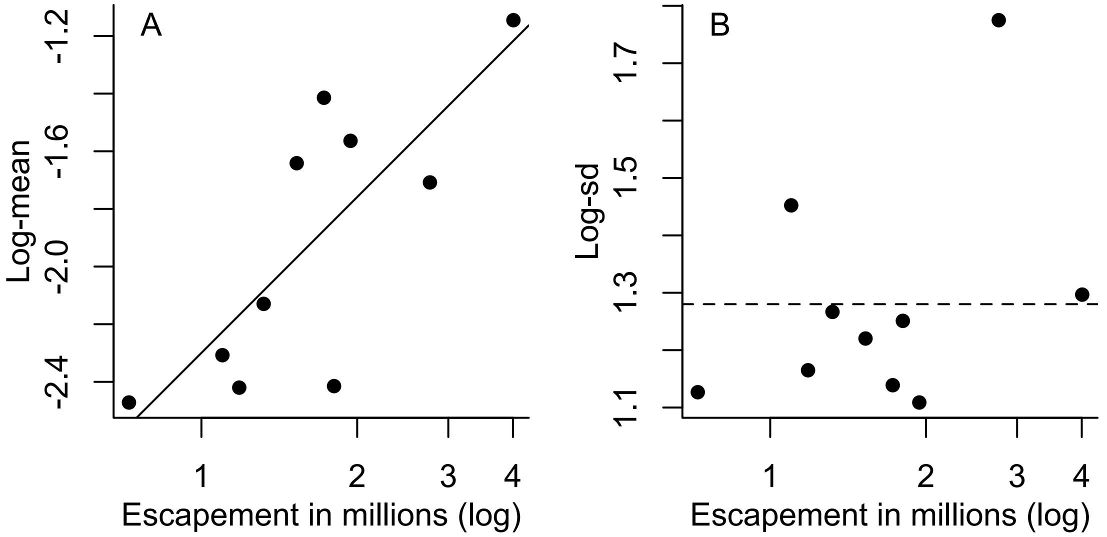
Appendix B: Supplementary material for Chapter 2

Supplementary Table 1: Model selection table for models fit the growth response of resident fish as a function of sockeye salmon spawning density in streams. Models were fit to all combinations of Arctic grayling and rainbow trout in Hidden and Lynx creeks.

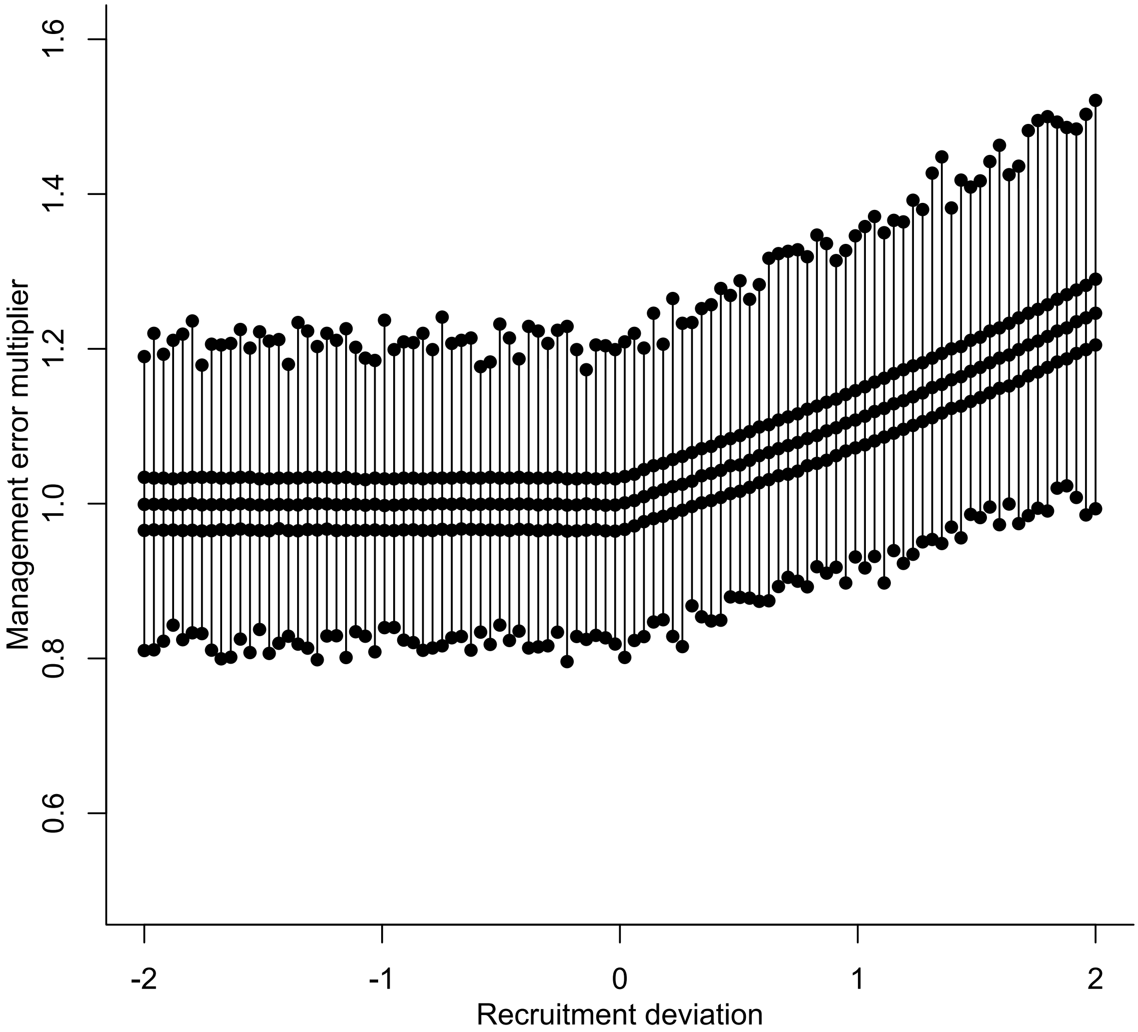
Model	K	AIC	ΔAIC
Arctic grayling, Hidden Creek			
Sigmoid	**6**	**-5234.41**	**0.00**
Saturating	5	-5228.02	6.39
Linear	4	-5225.80	8.61
Arctic grayling, Lynx Creek			
Sigmoid	**6**	**-2383.08**	**0.00**
Saturating	5	-2379.52	3.56
Linear	4	-2379.28	3.81
rainbow trout, Hidden Creek			
Sigmoid	**6**	**-11284.78**	**0.00**
Saturating	5	-11276.66	8.11
Linear	4	-11275.43	9.35
rainbow trout, Lynx Creek			
Sigmoid	6	-12490.96	0.58
Saturating	**5**	**-12491.54**	**0.00**
Linear	4	-12483.06	8.48

Supplementary Table 2: Mean parameter estimates (95% confidence intervals) for the best model for each of the species-stream combinations. g_0 is the growth rate at a spawning density of zero, g_m is the maximum growth rate, s_0 is the sockeye spawning density that produces have saturation, and b is the steepness of the sigmoid curve. When $b = 1$, the relationship follows a saturating function.

Model	g_0	g_m	s_0	b
Arctic grayling, Hidden Creek				
Sigmoid	*0.005*	*0. 003*	*0.207*	7.79
	(0.004,0.006)	*(0.002,0.004)*	*(0.179,0.255)*	(4.01,112.37)
Arctic grayling, Lynx Creek				
Sigmoid	0.0046	*0.003*	*0.157*	6.11
	(0.004,0.005)	*(0.002,0.004)*	*(0.148, 0.209)*	(1.00,202.60)
Rainbow trout, Hidden Creek				
Sigmoid	*0.013*	*0.007*	*0.196*	*10.98*
	(0.012,0.015)	*(0.0.005,0.009)*	*(0.179,0.232)*	*(6.03, 184.61)*
Rainbow trout, Lynx Creek				
Saturating	*0.010*	*0.016*	*0.289*	…
	(0. 007,0.011)	*(0.012,0.024)*	*(0.066,0. 449)*	



Supplementary Figure 1. The relationship between the mean (A) and standard deviation (B) of the lognormal distribution of individual stream densities as a function of escapement. The log-mean was significantly related to escapement (R^2=0.55, $p < 0.01$). There was no significant relationship between the standard deviation and escapement (R^2=0.04, p=0.28). We used the average standard deviation (dashed line) in stochastic simulations.



Supplementary Figure 2: The management implementation error multiplier as a function of recruitment deviations. Larger runs tend to lead to escapement above the target. In stochastic simulations, for each year, the escapement target is multiplied by a random draw from a lognormal distribution. The mean of this distribution increases with large recruitment deviations according to a piecewise function. The points represent the 0.025, 0.25, 0.5, 0.75, 0.975 quantiles, from bottom to top.

Appendix C: Supplementary Material for Chapter 4

Supplementary Table 1: Model Selection for dynamic factor analysis models evaluating common patterns in time series of commercial fisheries catches in 60 stocks around Alaska Stocks are delineated by species or species group and area harvested. We tested up to two trend models. We considered two error structures; where all stocks share a single observation error (DE), where all stocks have individual observation error (DUE). A one-trend model indicates the most commonly shared trend among the 60 time series of commercial fisheries catches.

Number of trends	Error structure	Num. parameters	AIC	ΔAIC
1	**DE**	**61**	**5643**	**0**
1	DUE	120	5732	89
2	DE	120	5678	35
2	DUE	179	5720	77

Supplementary Table 2: Model Selection for dynamic factor analysis models evaluating common patterns in time series of commercial fisheries revenue from 105 Alaskan communities We tested up to two trend models. We considered two error structures; where all stocks share a single observation error (DE), where all stocks have individual observation error (DUE). A two-trend model indicates the two most commonly shared trends among the 105 time series of commercial fisheries revenue.

Number of trends	Error structure	Num. parameters	AIC	ΔAIC
1	DE	106	6972	1316
1	DUE	210	6361	884
2	DE	210	6257	599
2	**DUE**	**314**	**5658**	**0**

Supplementary Table 3: Regression results explaining changes in community revenues against changes in catch and changes in price Changes in revenue are measured as the percent change in revenue from commercial fishing for each community from before (1980-1989) and after (1990-1999) the regime shifts. Changes in catch are measured as the percent change in catch (pounds harvested) from commercial fishing for these same years. Percent changes in price are computed from prices weighted by the proportion of commercial harvest by weight. To assess relative strength of covariates, effect sizes were computed using a separate regression of z-score standardized variables. Best model includes full main effects and interaction terms. The full model explains 93% of the variation in in change in revenue (R^2=0.9268, $p < 0.001$).

Covariate	Coefficient	Std. Error	P-value	Effect Size
Intercept	-6.790	2.295	<0.0001	
Change in catch	0.913	0.040	<0.0001	1.19
Change in price	0.801	0.060	<0.0001	0.84
Interaction between change in catch and change in price	0.008	0.001	<0.0001	0.43

Supplementary Table 4: Model selection for regression analysis of changes in revenue in response to different types of diversification We tested richness (the number of fisheries) and diversity (a combination of richness and evenness as measured by the Reciprocal Simpson's Index). Both variables are $\log_{10}$ transformed. To assess relative strength of covariates, effect sizes were computed using a separate regression of z-score standardized variables.

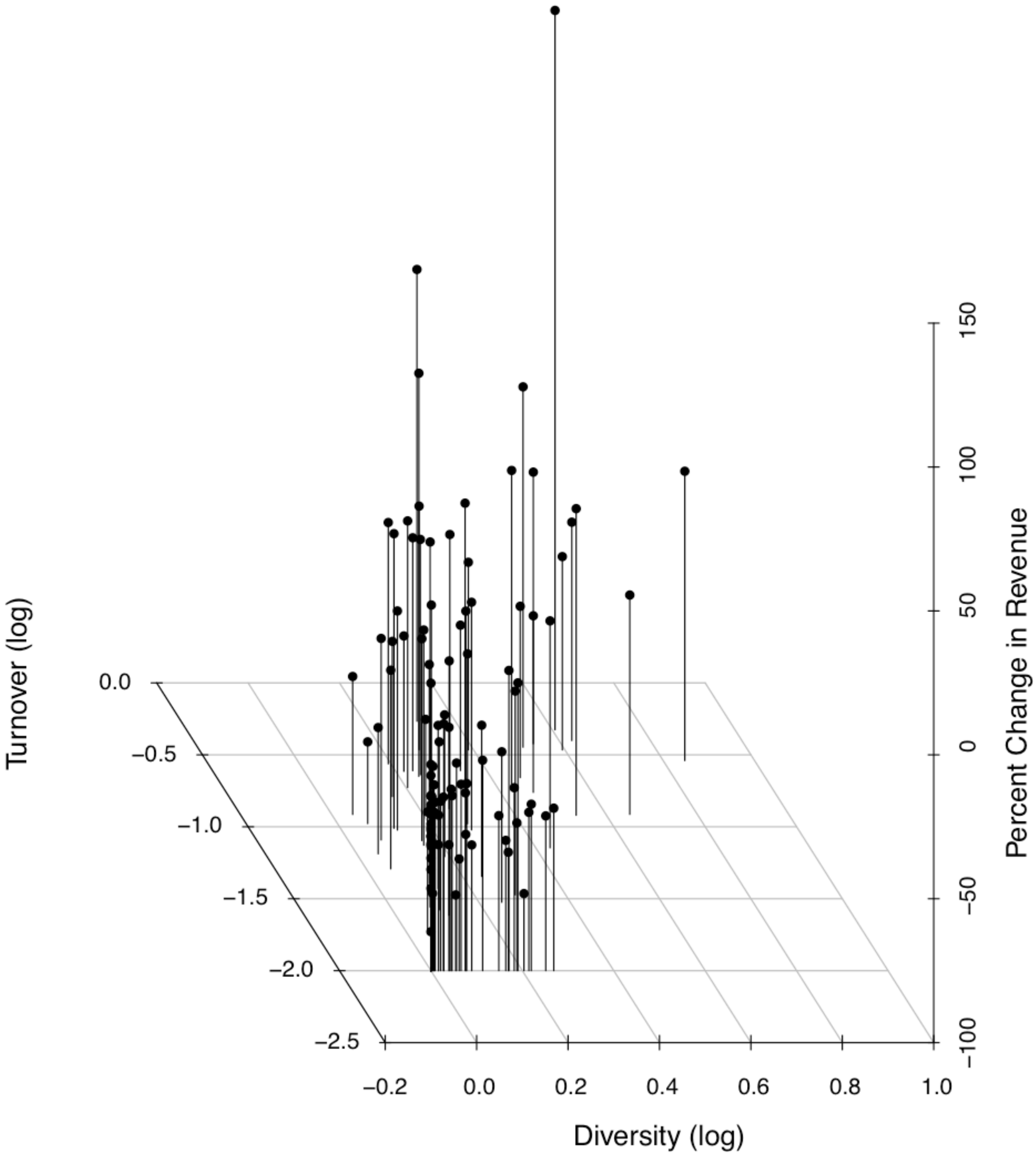
Model Covariates	Number of parameters	AIC	ΔAIC	Effect Size
Number of fisheries (richness)	2	735.9	6.0	9.9
Diversity	**2**	**729.9**	**0**	**13.7**

Supplementary Table 5: Regression model selection for changes in revenue as a function of diversification and turnover Changes in revenue are measured as the percent change in revenue from commercial fishing for each community from before (1980-1989) and after (1990-1999) the regime shifts. Diversification is measured as Reciprocal Simpson's Diversity ($\log_{10}$) and turnover is measured using Jaccard's Dissimilarity index ($\log_{10}$).

Model covariates	Number of parameters	AIC	ΔAIC
Diversification	2	1001.7	5.66
Turnover	2	1001.6	5.65
Diversification + Turnover	3	999.58	3.54
Diversification + Diversification*Turnover	**3**	**996.04**	**0**
Diversification + Turnover + Diversification*Turnover	4	997.66	1.62

Supplementary Table 6: Regression parameters for the best linear model fit for changes in community commercial fishing revenues as a function of diversification and turnover Changes in revenue are measured as the percent change in revenue from commercial fishing for each community from before (1980-1989) and after (1990-1999) the regime shifts. Diversification is measured as Reciprocal Simpson's Diversity ($\log_{10}$) and turnover is measured using Jaccard's Dissimilarity index ($\log_{10}$). To assess relative strength of covariates, effect sizes were computed using a separate regression of z-score standardized variables. The best model includes main effects on diversification and interaction terms. The full model explains 26% of the variation in in change in revenue (R^2=0.26, $p < 0.00001$).

Covariate	Coefficient	Std. error	P-value	Effect size
Intercept	-41.43	3.965	<0.0001	
Diversification	123.5	21.78	<0.0001	0.307
Diversification*Turnover	71.52	25.81	<0.01	0.187



Supplementary Figure 1: Diversification and turnover of fishing opportunities buffer against abrupt shifts Observed changes in revenues from before (1980-1989) and after (1990-1999) are plotted against diversity and turnover of fishing opportunities for 105 Alaskan fishing communities. Diversity, as measured by the reciprocal of Simpson diversity (log scale), indicates total portfolio size and distribution among component stocks (often referred to as alpha diversity). Turnover (often referred to as beta diversity) is Jaccard’s dissimilarity index measuring changes in the in the relative contribution of stocks to a communities overall portfolio (by catch). Regression analysis indicates the best linear model between changes in revenue as explained by Simpson’s diversity and turnover includes a significant interaction ($R^2=0.26$, $p<0.0001$, Supplementary Table 5, Supplementary Table 6).